Irja Ida Ratikainen

# Foraging in a variable world: Adaptations to stochasticity

Thesis for the degree of Philosophiae Doctor

Trondheim, March 2012

Norwegian University of Science and Technology
Faculty of Natural Sciences and Technology
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# PREFACE

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February 2012

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II. **Ratikainen, I. I.**, Sødal, L. R. H., Wright, J. & Kazem, A. J. N. (Provisionally accepted) Information-gathering strategies in wild Siberian jays: optimal sampling and private versus public information use. *Animal Behaviour.* [2]

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[1] JW and AJNK initiated the project. IIR, JW and AJNK planned the experiment. IIR performed the experiment with technical assistance. IIR analyzed the data and wrote the manuscript with help from JW and AJNK.

[2] JW and AJNK initiated the project. IIR, JW and AJNK planned the experiment. IIR performed the experiment with technical assistance. LRHS and IIR analyzed the data. IIR wrote the manuscript with help from JW and AJNK.

[3] DS, IIR and GG performed the experiments. DS analyzed the data. DS wrote the manuscript with help from IIR, JW, GG, DB and LH.

[4] IIR and JW initiated the project. IIR performed the data gathering with technical help, analyzed the data and wrote the manuscript with help from JW.

[5] JW initiated the project. JW and IIR wrote the manuscript.

# INTRODUCTION

Much of the theory behind behavioral ecology and life history evolution involves optimal choices based upon aspects of either the environment, the individual or other members of the group or population. However, many of the details may not be known with certainty by the individual, mostly because the world is a variable place. Environments are heterogeneous and change over time and space, and decisions must often be based upon uncertain or missing information. Living in times when environmental climate change is threatening naturally begs answers to questions about how animals will cope with increasing environmental variability. In order to understand this, it is important to first understand how animals cope with stochasticity in their natural and social environment.

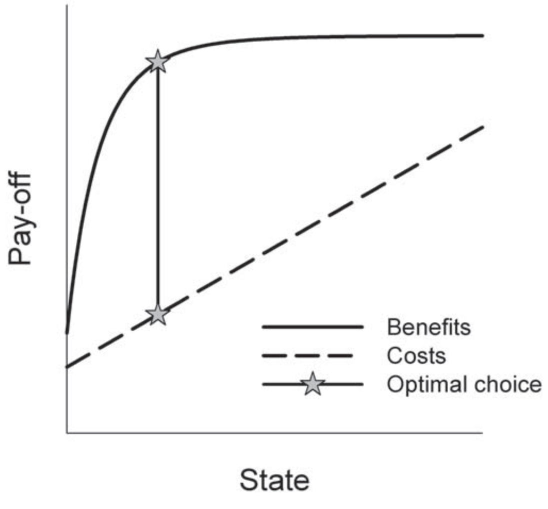

**Figure 1.** In classical behavioural ecology the optimal choice is found by comparing cost and benefits of each strategy. The optimal choice is not the strategy (here a continuous choice of states along the x-axis) with highest benefits, but the strategy with the largest positive difference between benefits and costs.

Animals encounter stochasticity and uncertainty in most of their daily decisions including foraging, which is a very important part of any animal's life. There are many ways to cope with the uncertainty, depending on the timescale and the predictability of the environment. On relatively short timescales, variability may be encountered as fluctuations in food availability, and optimal foraging theory has long been concerned with the patch and prey choices of animals given certain characteristics of their environment. As in most other areas, the theoretical foundation here is largely based on optimality models that do not take stochasticity into account (Fig. 1). It has become clear, however, that predictability and variance in the environment can affect outcomes and adaptations in a number of ways (Dall, 2010; Stephens, 2007).

### *Variance sensitivity*

If fluctuations in resources are completely stochastic (i.e. unpredictable) and no information about the current state is available, the best strategy should be to use variance sensitivity (Caraco et al., 1980; Stephens and Krebs, 1986; also known as risk sensitivity, see Ydenberg, 2007 and chapter V for discussion on terminology). This strategy is based on Jensen's inequality, which states that if F(x) is a concave function, then $\mathrm{E}[F(x)] \leq F(E[x])$. This is easily seen in Fig. 2. It is a simple corollary that the opposite is true for convex functions. In practice this means that strategies with lower variance in pay-off will give higher mean fitness when the relationship between the pay-off and fitness (utility function) is concave as in Fig. 2 (McNamara, 1996; Smallwood, 1996). In variance sensitivity theory, these are known as variance-averse strategies. If the utility function relating pay-off to fitness is convex, then variance-prone strategies (i.e. strategies with

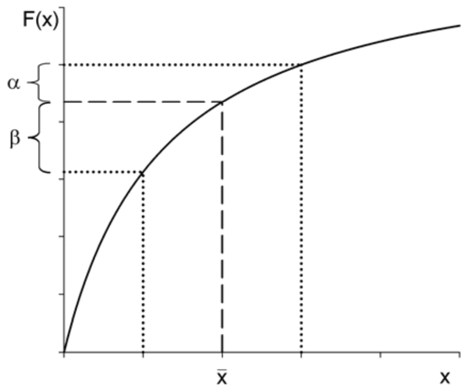

**Figure 2.** Illustration of Jensen's inequality. If F(x) is a concave function of the variable x, then the mean of F(x) is smaller than F(mean of x), because the negative deviations affect the mean of F(x) more than the positive deviations (α<β).

relatively high variance in pay-off) are predicted to be better, because the mean fitness will be higher with larger variance around the mean.

Starvation is usually suggested to be the force that creates non-linearity in the utility function that relates pay-off to fitness, because starvation probability as a function of energy reserves, may be declining slower with increased energy reserves. Individuals that are on a negative energy budget (i.e. on average receiving less food than that required for survival) are likely to fall below the starvation threshold, and should therefore be variance prone (Bednekoff and Houston, 1994; Stephens, 1981). Similarly, individuals on a positive energy budget should be variance averse in order to minimize the risk of falling below the starvation threshold. The empirical evidence for the energy budget rule is not conclusive (Bateson, 2002; Kacelnik and Bateson, 1996), but recent more comprehensive studies do provide some supporting results (Mayack and Naug, 2011). In addition to starvation, there may also be other factors which create non-linearity in the utility function. Reproduction has been suggested to be the most likely candidate, as it is possible that parents need a certain amount of reserves in order to be able to reproduce (Bednekoff, 1996; Hurly, 2003; McNamara et al., 1991). Few empirical tests of this exist (but see Hurly, 2003).

### *Sampling*

Even though sampling frequently carries costs, often due to lost opportunities of foraging in patches of known profitability, it may be possible to increase fitness by sampling patches and using the information gained to increase future and therefore mean pay-off from foraging (Dall and Johnstone, 2002; Lima, 1984; Lima, 1985; Stephens, 2007). Therefore, variance sensitivity is predicted to be abandoned in favour of sampling whenever the environment is less stochastic and more predictable, and therefore provides reliable information (McNamara, 1996). Sampling may be carried out via direct interaction with the environment, in which case the resulting information is called 'private information' and is usually of relatively high quality. Information may also be gained by observing the foraging success of group members or other conspecifics, although the 'public information' that is obtained is often less reliable (Templeton and Giraldeau, 1996; Valone, 1989).

Information may be used in different ways, either through very simple 'rules of thumb' (McNamara and Houston, 1980) that are only based upon currently available information, or through more sophisticated rules based upon a combination of information obtained over longer time periods. A well-known example of a simple rule of thumb is the 'win-stay lose-shift' strategy, stating that if the reward currently obtained is above some threshold, then the animal should stay in the current patch, but if the pay-off is below the threshold, then it should shift to a new patch (Bicca-Marques, 2005; Olton and Schlosberg, 1978). In environments that are more complex, such a simple rule may lead to erroneous decisions because a single foraging event provides insufficient information. In such environments, more complex decision rules can be more profitable. Linear operator rules (Devenport and Devenport, 1994; Gross et al., 2008) and Bayesian updating rules (McNamara et al., 2006; Olsson and Brown, 2006; Valone, 2006) are often considered in the literature to be better alternatives when dealing with more variable and complex environmental cues. Both of these alternatives are classes of behavioural rules that incorporate both recent and previously obtained information in a way that puts greater emphasis on more recent information, since older information is less reliable and is thus discounted with time. Empirically there are many studies that support such a use of information in foraging (Giraldeau, 1997; Nonacs and Soriano, 1998; Tamm, 1987), and even though the existence of simple win-stay lose-shift strategies has been established, there is generally more support for more complex rules of thumb (Valone, 2006).

### *Behavioural flexibility and body mass regulation*

The most obvious adaptation to a variable environment is, of course, to change behaviour according to the operating conditions. In foraging, such behavioural flexibility can be manifested as ecological tracking that, in its simplest form, constitutes an omniscient animal that will always forage in the most profitable patch (Stephens, 2007). This area of foraging theory is reasonably well explored (Stephens and Krebs, 1986; Stephens et al., 2007), because it requires only that the individual changes behaviour when the environment changes rather than always perform the action that is optimal in the average environment, providing there is no additional cost of changing strategy that outweighs the benefit.

The adaptive regulation of body mass by small birds in winter has been well explored both empirically and theoretically (e.g. Brodin, 2007; Brodin and Clark, 2007). Because of mass-dependent predation and other mass-dependent costs, it is not optimal for birds to carry excessive levels of fat reserves (Witter and Cuthill, 1993). However, depending on the energetic requirements expected in the near future, the balance between the costs and benefits of fat reserves changes with the environment. Small birds are therefore expected to adjust their body mass according to important factors such as predation, day length and weather conditions (Brodin and Clark, 2007). An individual's social status in a group may also affect both access to food and predation risk and individuals of low dominance rank are often predicted to maintain higher fat reserves because of their poorer environmental conditions (Clark and Ekman, 1995; Ekman and Lilliendahl, 1993).

Behavioural flexibility is also necessarily important for animals to be able to utilize the information they obtain by sampling. Sampling and behavioural flexibility are therefore undeniably tied together.

### *Configural vs. featural cues*

Integral to behavioural flexibility is the ability of the animal to separate between different patches to forage in, or different conditions. To do this animals use cues, defined as any feature of the world that can be used to guide future actions (Hasson, 1994). Such use of cues is taken for granted in many studies of foraging ecology, but there are good reasons for believing that different types of cues have evolved to be used in different situations.

Many different cues may be available, and a coarse categorization is the division between featural and configural cues. Featural cues include any feature of a patch or object such as its colour, shape or size, while configural cues are the absolute or relative spatial positions of any object or patch. Despite the fact that cue use is an integral part of foraging and patch choice, the differential use of these different types of cues have not previously been of much concern to behavioural ecologists, but the topic has been investigated within the tradition of small scale spatial cognition. Preferential use of one type of cue over others may be predicted based on the general ecology of a species. It is often predicted that food storing species, to a much larger degree than other species, rely upon spatial (i.e. configural) cues to find food (e.g. Brodbeck, 1994; Clayton and Krebs, 1994), but this has not been unambiguously confirmed experimentally (e.g. Carter et al., 2010; LaDage et al., 2009 and discussion in chapter III).

### *Insurance and body mass regulation*

Insurance strategies are strategies that minimize the likelihood of costly events by either reducing the probability or the cost of the event (Dall, 2010). Generally, the concept of insurance can be understood as a trade-off between current net pay-off and the costs of adverse effects such as bad weather and predation. A well known type of insurance is the maintenance of energy reserves above the level that is required in the current environment (Brodin, 2007; Brodin and Clark, 1997; Brodin and Clark, 2007). In addition to adjustment to expected changes in energetic demands (discussed above), there may be unexpected changes and hence the optimal body mass will often be greater than currently required (Brodin, 2007; Dall, 2010). This insures against severe effects of unexpected energetic demands

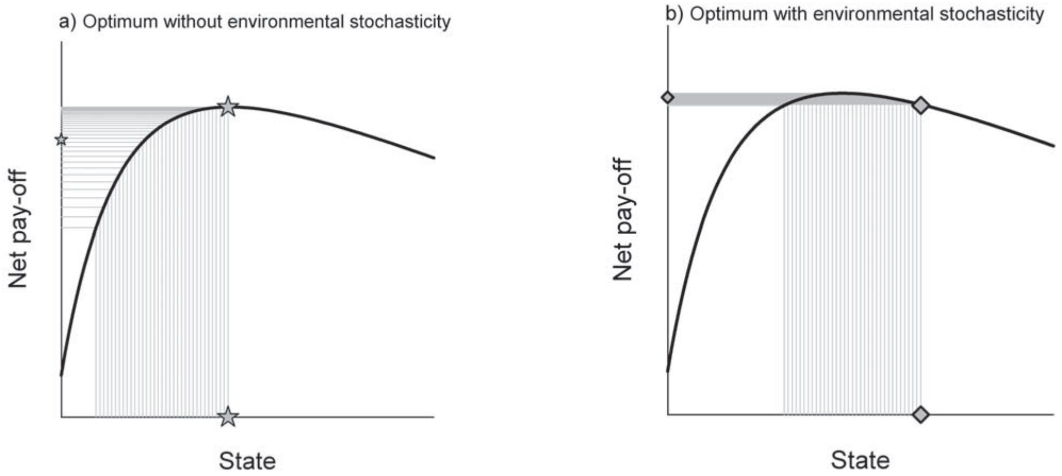

**Figure 3**. An illustration of the insurance principle. The curve is equal to the net benefit in Figure 1. The star indicates the optimum from Figure 1, and is found where the net benefit (benefits – costs) is largest. In **(a)** environmental variation, represented as grey lines, affects the state asymmetrically (only in negative direction); this could be the case for e.g. body mass where unpredictable events will never force body mass above the target set by the animal, but can frequently reduce body mass through increased energetic demands or decreased food availability. When unpredictable environmental variation is introduced, the mean net pay-off is reduced, as marked by the star on the y-axis. A new optimum (target) can then be found at an increased state, marked by the diamond **(b)**. Even though the new optimum (diamond) receives lower net pay-off, this new optimum will not be negatively affected by the variation (grey lines), and the mean net pay-off will therefore be higher for the new target state (diamond on y-axis in **b**).

produced by events such as cold periods. Body mass may be a special state because it is likely to be relatively easy to avoid unexpected increases in body mass, but due to reduced access to food or increased demands, body mass may unexpectedly drop to a level lower than preferred. Because of this, a higher target body mass will allow a high pay-off or survival probability even when environmental variation reduces body mass to levels below the target (Fig. 3). In seasonal environments it is often the case that both predictable weather conditions decrease while unpredictability increases towards winter. Low social dominance rank may also decrease the predictability of access to food (Clark and Ekman, 1995). This leads to an increase in the optimal body mass due to both increased energetic demands and due to insurance effects.

### *Adaptations to stochasticity in general*

The adaptations to stochasticity discussed so far occur at relatively short timescales involving behavioural responses to variable environments. At longer timescales it may be adaptive to respond to environmental variability with more permanent and therefore more efficient changes. Although there has been growing interest in the topic (Frank, 2011; McNamara et al., 2011; Meyers and Bull, 2002; Simons, 2011), evolutionary theories describing adaptive responses to environmental stochasticity remain scarce, are not well integrated into general evolutionary theory, and perhaps most importantly the specific theories are not well integrated with each other.

A few interesting connections have already been made between different types of behavioural adaptations to stochasticity. For example some authors have suggested that there is a smooth integration between insurance and sampling, as foragers must be insured (have large enough reserves) to be able to afford the possible energetic shortfall from sampling, because the pay-offs from such information gathering are inherently variable (Dall and Johnstone, 2002). Another example is the relationship between variance sensitivity and sampling. In addition to the predicted switch from variance sensitivity to sampling once environmental variation becomes in some way predictable, there is a more intricate relationship between these two types of adaptation. The switch point between variance-prone and variance-averse behaviour may shift due to uncertainty about the state of the environment at a larger scale. Such uncertainty may best be reduced by sampling patches that give reliable information about the environment and if that is given by less variable patches more variance aversion is expected when there is more uncertainty (McNamara, 1996).

There is little doubt that many such interesting connections could be made between different areas of evolutionary theory dealing with environmental stochasticity, in addition to the development of new theory to cover the areas with few formal hypotheses.

# AIMS

The main aim of this thesis was to study behavioural strategies that have evolved as a response to different levels of environmental variance and to put this knowledge, and the knowledge from the large body of literature that exists, into a wider context including all adaptive responses to environmental stochasticity. This was accomplished by studying the foraging behaviour of an avian model system and reviewing and synthesizing the relevant literature. More specifically, the research questions I attempted to answer included:

a) How do Siberian jays use variance sensitivity and sampling as behavioural responses to different levels of predictability? (papers I and II)

b) How do Siberian jays and other birds use information from cues to choose the most profitable patch in variable environments? (papers II and III)

c) How do Siberian jays and other birds adjust foraging and body mass to predictable environmental variation? (papers III and IV)

d) How are behavioural responses to environmental stochasticity related to responses at evolutionary timescales? (paper V)

# GENERAL METHODS

### *Siberian jay study population*

The Siberian jay (*Perisoreus infaustus*) is a relatively small, resident Corvid living in old boreal forest in Eurasia. The species is highly territorial, defending the same territory year round. A territory contains a single group, typically composed of two to five birds. Groups consist of a breeding pair that is usually accompanied by their offspring from previous years and immigrants from other groups (Ekman et al., 1999). Offspring of the breeding pair sometimes forego dispersal, and may remain in their natal territory for several years. Parents behave nepotistically, acting less aggressively toward their offspring compared to immigrants. This results in higher winter survival for retained offspring compared to immigrants (Ekman et al., 2000; Griesser et al., 2006). During autumn the jays hoard large amounts of food that are stored in numerous small caches and used for overwinter survival. Breeding may start as early as April, even before the snow cover has disappeared. Siberian jays are considered opportunistic foragers and their varied diet consists of fungi, berries, insects, spiders, snails, murid rodents and carrion (Andreev, 1978; Borgos and Hogstad, 2001). The birds participating in the studies presented in this thesis (papers I-IV) were part of a large wild study population outside Arvidsjaur in Northern Sweden (65º 40`N, 19º0`E; Figure 5). Individuals were colour banded, sexed molecularly and their social status classified as 'breeder', 'retained offspring' or 'immigrant', as part of this long term project (Ekman et al., 2000; Ekman et al., 2002). Siberian jays are easily habituated to human presence, and all birds participating in these experiments readily took food items at very short distances.

**Figure 5.** The study area of the Siberian jays is found outside Arvidsjaur in Northern Sweden, marked on this map by the feet of the bird.

**Figure 4.** The main study species, the Siberian jay. (Photo by Eirik Grønningsæter)

### *Additional study populations*

In study III we also present results from experiments with two further species, the Kea (*Nestor notabilis*) and the noisy miner (*Manorina melanocephala*). The Kea is an opportunistic and innovative parrot (family Strigopidae) native to New Zealand. They live in large social groups. The noisy miner is endemic to eastern Australia. It is an omnivorous and cooperatively breeding honeyeater that feeds on both nectar and invertebrates. Experiments with both species were performed in captivity.

### *Experimental feeders*

For the experiments on Siberian jays in studies I-III two types of feeders were used: (a) a feeder consisting of three long tubes or (b) a large one-shot feeder. The three long tubes were placed next to each other giving the jays three choices differing in colour code and spatial position. The food was delivered to the jays through the tubes by the experimenter. The one-shot feeders consisted of several boards with up to 16 small tubes sunken into the surface. In each tube a single reward was provided. The tubes could be closed and had opaque lids to conceal their contents, and were coded with rubber collars of differing colours to signal information about the contents of the tube. This type of feeder allowed us to present the jays with both randomly distributed choices and clusters of equal choices constituting a ‘patch’. In all three experiments we used three colours coding for three levels of variance in reward size: ‘no variance’, ‘low variance’ and ‘high variance’. In studies I and III no further information was provided, but in study II patches consisting of four tubes with the same colour also contained rewards of the same size and therefore potentially provided additional reliable information about reward size once one tube in a patch had been opened.

The Kea and the noisy miners were presented with other specific types of feeders in captivity to test what type of cues they used to choose their food source. These feeders are described in detail in paper III.

### *Other field methods*

For the Siberian jays, most training and experiments were performed during repeated sessions lasting from 30 min to approximately 60 min. Because the studies were performed during the caching period in the autumn, each group member visited the food source (feeder or other) roughly 10-30 times during one such session, and made repeated choices between the three options that were available to them. On most days each group experienced one or two training or experimental sessions.

In addition to the introduction of the experimental feeders, each year the jays were also trained to take small pieces of sausage from a top pan balance, allowing us to collect repeated measures of individual body mass without handling the jays. Within a maximum of ten minutes before each session we obtained body mass data for all individuals if possible.

# MAIN RESULTS AND DISCUSSION

### *Behavioural responses to stochastic variation*

In paper I, our experiment with Siberian jays clearly demonstrates that they are variance sensitive. In addition, the energy budget rule receives some support in that individuals in different states differed in their variance sensitivity. However, it was not the commonly considered fat reserves that proved to be the important state here, because we found no difference in strategies between individuals of different body mass; rather, there was an indication that reproduction was the factor creating the relevant threshold as breeders had variance-prone preferences, while immigrants were variance averse (paper I).

Despite this clear support for the tested hypotheses, these results still suggest many new questions. We find that breeders are variance prone and immigrants are variance averse. The suggested reason for the difference is a differently shaped utility function, due to breeders having an additional energetic demand threshold for reproduction in the following season (paper I). Although it is well known that only the breeding pair reproduce and the other individuals in the group do not help at the nest, we have no further evidence for a difference in utility functions. It would be reassuring if further work could confirm this. More importantly, our results do indicate that the suggested threshold due to reproduction is a real possibility under natural conditions and hopefully may inspire more research on other species where this could be likely.

It is expected that variance sensitivity should be abandoned in favour of sampling when the variation in food patches becomes in any way predictable. This is supported by the results in paper II, which show that Siberian jays sample patches for information and use both personal and public information to increase profitability above that which could be expected by foraging without sampling (paper II).

Another way of dealing with unpredictable environmental variation is to use insurance strategies. Although the use of insurance strategies was not directly tested in this thesis, paper IV does provide some support for increased body mass as insurance among the jays. Birds were heavier as winter approached, and the increase in mass appeared to be larger than that required by the decreased environmental conditions during the study period (true winter fattening sensu Lehikoinen, 1987). However, this is exactly as expected if winter is a more variable season, which is likely given that snow cover decreases the availability of predictable food. In addition, operational temperature measured as wind chill were more variable toward the end of our study period (paper IV), indicating more variable weather and energetic demands. The jays are thus better prepared for unexpected cold days or nights with larger reserves of fat.

### *Behavioural responses to predictable variation*

Provided animals possess the information necessary, it is expected that they change their behaviour to fit current conditions unless such behavioural flexibility is too costly for other reasons. In paper II we show that the Siberian jays used the information they obtained about the food patches to increase their pay-off. However, they did not use the information in the way that would provide the highest pay-off at any point in time. Instead they continued sampling throughout the experimental sessions.

In paper III we show that three different species of bird have unequal preferences for the type of cues used in choosing food sources, but find no pattern consistent with general ecology as the driving force behind the differences. Siberian jays and noisy miners both seemed to prefer configural cues over featural cues when the two were placed in conflict. Keas on the other hand preferred featural cues over configural cues. It is not obvious what separates the Kea from the two other species, but we note that while all three species are generalist foragers, the Kea is very innovative and routinely exploits novel food sources, and suggest some hypotheses for further investigation. We propose that the spatial scale is important in the choice of cue, configural cues being more important at large scales while featural cues may be more important at smaller scales. This has to our knowledge never been tested, and if we find that patch choice is made using configural cues while prey choice within patches is based upon featural cues, this could be an important tool allowing insight into which choices the animals consider to be problems of patch vs. prey choice, as conceived by classical optimal foraging theory.

In paper IV we present indications that Siberian jays adjust their body mass in expectation of predictable environmental variation. The observed body mass regulation is indicative of a highly flexible strategy in foraging and energy use, as expected given the variable environment inhabited by this species. The results of paper IV show that the jays increase their body mass over the day, towards the winter and during periods of colder weather.

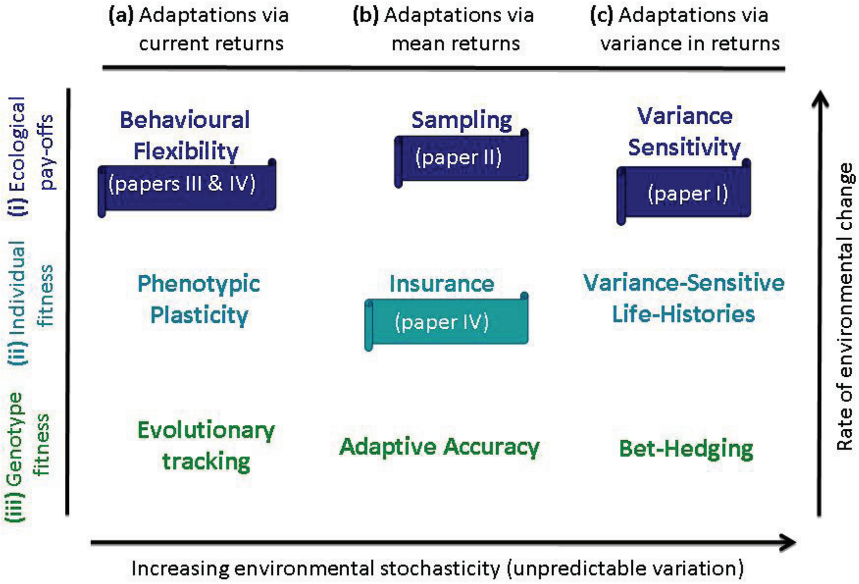

**Figure 6.** A simplified version of the conceptual framework presented in paper V. In this version, I have highlighted where the different studies (paper I-IV) fit into this framework. They all investigate adaptations at the behavioural time scale, with relatively fast rate of environmental change and ecological pay-offs (level (i) in papers I-III and paper IV originally classified at level (ii) but aspects are also close to level (i)). The studied adaptations span the range of stochasticity from relatively predictable (a), with adaptations expected to maximize current returns, through more unpredictable variation where adaptations are expected to maximize mean returns (b), to highly stochastic environments where adaptations are expected to affect fitness through variance in returns (c).

These results concur well with predictions from models and results from previous studies. In addition we found that large breeders have relatively low body mass compared to subordinates, while small breeders have relatively high body mass. This result is a bit more puzzling, but may be due to differing constraints, such as other activities including territory defense and vigilance, between breeders and less dominant birds in the group (paper IV).

### *Long term responses to stochasticity*

Behavioural responses to environmental stochasticity are only effective at short timescales. They are therefore clearly only part of a larger set of responses used over longer time periods (Fig. 6). Other adaptations to environmental stochasticity differ according to both the degree of unpredictability involved and the rate of environmental change. In paper V we ambitiously attempt to summarize and compare all of the different adaptations to stochasticity by creating a framework that separates adaptations according to the timescale of their employment and the type of effect they have on the returns, ranging from effects on current return, through effects on mean return to adaptations with effects on variance in returns.

At the ecological timescale, pay-off can be maximized in the long run by behavioural adaptations ranging from behavioural flexibility through sampling to variance sensitivity (Fig. 6 i a-c). At the level of individual fitness (Fig. 6 ii a-c), irreversible phenotypic plasticity is a well known adaptation to maximize current returns (e.g. Piersma and Drent, 2003 and paper V), while insurance strategies maximize mean overall individual fitness (e.g. Dall, 2010 and paper V), and what we have termed 'variance-sensitive life-histories' includes strategies that are adaptations to reduce within-individual variance in fitness components and thereby increase indvidual fitness (see paper V). At the evolutionary timescale (Fig. 6 iii a-c), genotype fitness is increased by evolutionary tracking that will maximize current genotype fitness (see Simons, 2011 and paper V). Adaptive accuracy is a measure of the mean genotype fitness including both the deviance of the target phenotype from the optimal phenotype and the variance around this (Hansen et al., 2006 and paper V). Lastly, bet-hedging strategies reduce the variance in individual fitness within the genotype. Our conclusions from this work include suggestions clarifying the differences between different types of adaptations such as within- and between-generation bet-hedging, and more importantly that both theoreticians and empiricists take stochasticity into account when studying adaptations, because it can be crucial to our understanding of many interesting problems in behavioural and evolutionary biology. A more structured categorization such as the one we present in paper V (see also Fig. 6) may help in revealing new areas of interest and fascinating connections between the different types of adaptations.

### *Rules of thumb and their study*

When animals forage in variable environments their decisions can be predicted by complex mathematical models, but we do not expect that any individual animal performs such complex calculations each time it makes a choice. Rather we expect them to use 'rules of thumb', which are mechanistic approximations to more complex optimal solutions (Stephens and Krebs, 1986; also termed 'ecological rationality', see Todd and Gigerenzer, 2000). These rules of thumb are simple decision rules that work well in the environment in which they evolved, but may produce very unproductive behaviour as soon as the animal tries to respond to an environment or a task that the rule of thumb did not evolve to handle (McNamara and Houston, 1980).

A series of experiments on patch choice in blue jays (*Cyanocitta cristata*) have revealed that they perform much better in situations where they are choosing between staying or leaving a patch, instead of a direct choice situation with two mutually exclusive options, even when both situations offer the same choice economically (Stephens and Anderson, 2001; Stephens and Dunlap, 2009; Stephens and Dunlap, 2011). The results show that this is likely due to the rules of thumb that these birds use when making their decisions. These rules of thumb perform well in natural situations such as patch leaving problems, but not in artificial problems such as the binary choices common in captive studies.

It has already been noted that Siberian jays adjust their body mass in relation to predictable environmental variation (above). Another interesting finding in paper IV is the behavioural rule they seem to use for adjusting to the coming weather conditions. Basic physiological processes dictate that body reserves must be adjusted in advance, and therefore body mass in this species correlates best with the wind chill measured 24 hours previously. Using the wind chill experienced at the same time of day on the previous day would appear to be a sensible simple rule of thumb, because it predicts current wind chill better than does the wind chill either 12 or 48 hours before.

In paper II we were explicitly interested in exploring the rule of thumb the jays used when they chose which patch to forage from. We were surprised to find that they did not use the win-stay lose-shift rule that would have been the most profitable rule in the experimental task we provided. This rule can also be considered a very simple rule of thumb, and should therefore not be hard for the jays to employ. However, it is evident that it is not the simplicity or the profitability in the experimental environment that affects the choice of rule of thumb, but rather the natural environment that the birds evolved to cope with.

Throughout the empirical studies with wild birds (papers I-IV) it has become evident that the precise conditions and design of the experimental manipulation are crucial in the interpretation of any resulting behavioural strategies. It has previously been pointed out that behaviours observed in laboratory experiments can be adaptations to the animal's natural environment, rather than the expected responses to the experimental set-up (McNamara, 1996; Stephens, 2008). For very similar reasons, it matters if the study is conducted in captivity or in the wild. Although it has not been a primary goal of my studies to investigate differences between results found in captivity and in wild animals, some of my results do indicate that there may be important differences (papers I, II and IV). Because most researchers are interested in adaptations to naturally occurring conditions, it is important to avoid erroneous conclusions about mal-adaptation based on experiments that test how animals solve problems they are not adapted to solve. It is clear that careful experiments in the laboratory can reveal interesting facts about how animals make their choices (e.g. Stephens and Anderson, 2001). The experiments presented in this thesis show that conducting experiments with wild animals solves part of the problem, because under natural conditions the animals are able to assess their own state (e.g. paper I). However, it is also important that the experimental task the animal is presented with closely matches their natural foraging situations; if it does not we must be careful in interpreting the results (e.g. paper II).

In total, the results from papers I-IV generally support the predictions of behavioural adaptations to increasing stochasticity. Clear evidence of variance sensitivity, sampling, and behavioural flexibility, is found. We also observe reasonable indications of insurance strategies in body mass management.

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# paper I

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# Social class influences degree of variance sensitivity in wild Siberian jays

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Variance sensitivity theory predicts that optimal foragers should take into account not only the mean but also the variance in rewards offered by alternative foraging options. Whereas a positive energy budget should favor variance aversion, a negative one should favor variance-prone choices. The risk of starvation is the most obvious fitness threshold that can select for variance-prone behavior, but additional thresholds may exist such as the energy required for reproduction. Previous studies of variance sensitivity have often been performed in captivity, and few have demonstrated the predicted state-dependent changes in individual variance preferences. We trained groups of wild Siberian jays (*Perisoreus infaustus*) to forage from one-shot feeders containing 3 color-coded options differing only in the variance of reward sizes. Not only did we find variance-sensitive behavior under natural conditions but also, for the first time, demonstrate the presence of significant differences in variance sensitivity within groups. Breeders exhibited a preference for high-variance rewards, whereas unrelated subordinates within the same groups preferred low-variance options. These results did not reflect risk of starvation (indexed by body mass) but might be explained by the additional energy needs of breeders compared with subordinates prior to the breeding season. *Key words:* food hoarding, food storing, optimal foraging, risk sensitivity, stochastic environment. *[Behav Ecol 21:1067–1072 (2010)]*

The world is a stochastic place due to variation in factors such as weather and the spatiotemporal distributions of food and predators. An optimal choice in foraging therefore includes consideration of not only the average or expected payoff but also the variation in those payoffs. Stochastic variance in foraging rewards may allow individuals to "gamble" for larger fitness returns than might be expected based solely on the average reward. The obvious risk is that more variable rewards are equally likely to provide much poorer fitness returns than the average. Theory on variance sensitivity, also termed risk sensitivity (see discussion of terminology in Ydenberg 2008) considers when such gambling or "variance-prone" behavior—as opposed to more conservative "variance-averse" behavior—might be adaptive (Real and Caraco 1986; McNamara and Houston 1992). More precisely, theory predicts that if fitness is not linearly dependent on energetic state, then the expected fitness increases from high versus low variance in intake rate are not the same, even if the average intake is the same (McNamara et al. 1991; Kacelnik and Bateson 1996).

The energy budget rule states that when animals are in poor energetic state relative to the state required for survival, variance-prone foraging will be favored and, conversely, positive energy budgets should generally favor variance-averse foraging (Stephens 1981). The reason for this is that when an animal is in an energetic state with high starvation probabilities each successive intake of energy provides accelerating probabilities of survival. Therefore, any stochastic (symmetrical) variation in foraging success will, on average, increase mean fitness outcomes. Animals in a relatively high energetic state, on the other hand, will obtain decelerating fitness returns from each unit of energy intake, and so variance in foraging success will on average decrease mean fitness. There is some evidence for the energy budget rule from laboratory studies showing state-dependent switches between variance-averse and variance-prone behavior, but the evidence is far from consistent (see Kacelnik and Bateson 1996, 1997).

It is, of course, not only the risk of starvation that can select for variance-prone behavior. McNamara et al. (1991) were the first to model how reproduction can affect variance sensitivity. A simple model by Bednekoff (1996) illustrates how variance-prone foraging is predicted below a threshold amount of energy required for individuals to reproduce, whereas variance-averse foraging is predicted once the state threshold has been reached. Essentially, any nonlinear relationship between an animal's state and its fitness should result in variance sensitivity (McNamara et al. 1991). We might therefore also expect variance-sensitive responses to other thresholds in (energetic) state, such as those associated with achieving and maintaining social rank (see Kuznar and Frederick 2003). However, there have been few experimental tests to confirm this generalized logic of variance sensitivity (but see Hurly 2003).

Because variance-sensitivity is expected to be highly state dependent, it is important that animals used in any experimental test are able to assess their own state in a context relevant to the situation in which the behavioral strategy evolved. This may be a problem for studies of variance sensitivity in the laboratory because it is hard to know how captive animals perceive and assess their own state. We cannot necessarily expect adaptive choices to be made by animals that do not have access to those features of the internal and external environment that they have been selected to use in assessments of their own state. It is therefore more plausible to assume that wild animals are able to assess their state in a way that is relevant to any experimental choices presented. However, there have been surprisingly few studies of variance sensitivity in the wild (but see Barkan 1990; Guillemette et al. 1992; Hurly and Oseen 1999; Hurly 2003).

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This study presented a wild population of Siberian jays (*Perisoreus infaustus*) with an experimental setup testing for variance sensitivity. We compare the foraging strategies employed by different classes of jays within social groups, and thereby test for differences in state thresholds between breeders versus subordinates as expected from theoretical models of variance sensitivity (McNamara et al. 1991; Bednekoff 1996; Hurly 2003). This design gave us a unique opportunity to explore the foraging decisions of animals in a natural environmental and social setting.

## MATERIALS AND METHODS

### Study species and population

The study population consisted of individually known color-banded Siberian jays in a forested area northwest of Arvidsjaur in northern Sweden (lat 65°40′N, long 19°0′E). The Siberian jay is a highly territorial bird that lives in small groups throughout the year. Groups consist of a breeding pair accompanied by retained offspring and unrelated immigrants (Ekman et al. 1999); the number of extra birds in a group is normally 1 or 2 but varies between 0 and 5. Approximately one-third of all offspring forego dispersal in their first year and may remain in their natal territory for several years. The immigrants in a group may be first-year birds or older birds that have delayed dispersal (Ekman et al. 1994). The nepotistic behavior of parents results in higher winter survival of first-year retained offspring as compared with first-year immigrants (Ekman et al. 2000; Griesser et al. 2006). Immigrants and retained offspring can easily be distinguished in the field by the differential behavior of the breeders, with the reliability of this method being confirmed genetically (Ekman et al. 1994). The species is sexually monomorphic and sex must be determined using molecular techniques (Ekman et al. 2000, 2002). The birds in this study were sexed and morphometric measurements taken as part of an ongoing long-term project. Siberian jays store food in the autumn, and the hoard is used for survival throughout the winter (Ekman et al. 1996). The diet is variable and includes fungi, berries, insects, spiders, snails, fish, and murid rodents (Andreev 1978; Borgos and Hogstad 2001). Caches made by one individual are in most cases later retrieved by the same individual (Ekman et al. 1996).

### Experimental procedure

This study population is well habituated to humans and readily takes food items, such as sausage or fat, at very short distances in the wild. In the current study, 6 groups of 2–5 birds were trained and tested between 2 October and 23 October 2007. One group consisted only of a breeding pair, whereas the remaining 5 groups all included 2 or 3 additional subordinate group members, with at least one of those being an unrelated immigrant (2 groups had 2 unrelated immigrants, 2 groups had 2 unrelated immigrants and one retained offspring, and the remaining group had one unrelated immigrant and one retained offspring). Each group was given access to an experimental feeder placed on the forest floor in their territory.

Feeders consisted of nine 60 × 60–cm horizontal boards, each containing an array of 16 equally spaced small tubes with lids sunken into the surface, placed together to form a continuous surface of 12 × 12 tubes (Figure 1). Around each tube lid was a collar made of a thin sheet of colored rubber that served as a potential cue to the contents of the tube. Although the tubes were semitransparent, the lids were covered with opaque tape so there was no possibility for birds to see what each tube contained.

As the birds were hoarding food at this time of year, a majority of visits to the feeder involved loading a single food item and flying away to cache temporarily in nearby trees (these temporary food caches are then repositioned in more permanent locations at a later time). In about a third of the cases (34.66%), individuals ate and/or loaded more than one food item during a single visit to the feeder. In such cases, the birds often simply opened the next tube closest to their initial choice, and these subsequent choices are not necessarily independent of the initial choice. By using only the first selection an individual made within a specific visit to the feeder, we are able to consider each visit as a separate choice event (see below). The feeder was large enough to allow several birds to alight and forage at the same time (Figure 1). In cases where dominant birds displaced subdominants, they just waited briefly in a nearby tree. Even if subordinates' actual or perceived access to the feeder were being influenced by the presence of dominant individuals, such perceived lack of control does not necessarily affect a subordinate's choice of which option to select first once it does gain access. There was no reason to believe that the simultaneous presence of others constrained the choices made by subdominants because the feeder was sufficiently large and tubes of different content types spaced such that a free choice of all options was available for all birds.

During an initial phase, the jays were trained to use 2 colors (red and blue) as cues indicating that a tube either contained a piece of sausage reward (two-thirds of the tubes) or that the tube was empty (the remaining third of the tubes). Sausage is a protein–fat food resource on which these jays have been shown to forage readily. Assignment of the 2 colors to the "full" versus "empty" conditions was counterbalanced across groups. All training and data collection were executed during sessions

**Figure 1**
The feeder as it looked during the experimental sessions: a total of 144 small tubes with opaque lids were evenly distributed over the feeder surface, with each tube having a collar made of a thin sheet of colored rubber. Different colors functioned as cues to different levels of variance, and the spatial distribution of colors was randomized and changed between each trial. Photo: Eirik Grønningsæter/WildNature.no.

of 30–60 min depending on the phase of the study. In the first training sessions, the lids were removed from tubes so the jays could see the reward inside. After all individuals had gained some experience with this and would pull the sausage out of the tubes, we proceeded by placing the lids loosely on top of tubes. This allowed the jays to still see the rewards inside but to obtain them they would first have to remove the lids. As soon as all individuals in a group readily removed lids to forage, we closed the lids fully so they had to be removed by the birds before they could discern and gain access to the reward inside. The sessions were then terminated when only 1 or 2 tubes with sausage had not been opened.

To be included in the study, each individual in each group had to achieve a color discrimination criterion by showing a strong preference (>90% of the lids opened during a session) for tubes with the collar color that indicated a food reward. Once all individuals in a group had passed this test, we proceeded to the variance-training phase. In this second training phase, we used 3 new colors to indicate 3 different levels of variance in the size of the food reward a tube contained. As there appeared to be an avoidance of yellow cues, the training and subsequent data collection phases used green, black, and purple as cues to the different levels of variance, and different groups were randomly assigned different combinations of the 3 colors to signify the different variances. A trinary choice was chosen over a binary choice because the former is closer to the natural situation (Hurly and Oseen 1999). Each of the 3 options occupied one-third of all tubes in a feeder, with tubes containing the different options randomly interspersed across the feeder. Within each group, the positions of the different colors within a feeder were randomized and changed between sessions.

In the color option indicating no variance, all tubes contained a reward of 2.5 g; in the medium-variance option, half the tubes contained rewards of 1.75 g and the other half 3.25 g; and in the tubes with high variance, half contained rewards of 1 g and the other half 4 g. Thus all variance options returned an equal mean reward of 2.5 g but the variance ranged from 0 to 0.56 to 2.25 in the no- versus low- versus high-variance options. For the first 5 sessions with variance training, groups were allowed as much time as required to deplete the feeders completely. This was to ensure that all individuals gained experience of all the colors and variance levels, even in the presence of any initial color preferences. The subsequent 10 sessions were used for data collection; in these, the feeders were removed after 30 min or whenever one color option was completely depleted, whichever occurred first.

Data were collected by recording all sessions using a digital video camera (Panasonic NV-MX500) mounted on a tripod approximately 1.5 m from the ground and at a distance of 3 m from the front of the feeder. Because it was hard to identify individuals on video, a stationary observer standing behind the camera provided the identity and position of each individual at the feeder continuously by way of a verbal commentary recorded onto the video. This also allowed the observer to comment on any unusual events out of shot that might affect the behavior of the birds but which could not be captured by the camera.

In addition, for 10 min preceding the start of every session, all individuals were allowed to take a few small pieces of sausage from a top pan balance. This enabled us to obtain the body mass of as many birds as possible at the beginning of each session. Body mass data were collected for 63% of birds on average (range: 0–100%) per group per session. All test and training sessions were performed between 8:30 in the morning and 16:30 in the evening, which are times when the jays are naturally active and foraging.

### Statistical procedures

General trends in individual variance sensitivity were explored by fitting a multinomial mixed model for ordered categorical response variables using the software MLwiN Version 2.02 (Rasbash et al. 2005). The response variable was variance level (low, medium, or high) selected in the first choice made during a specific visit, with social class of the individual within the group (breeder, offspring, or unrelated), sex, body mass, date, and time of day being tested as explanatory variables. We additionally tested for the effect of various measures of individual state as predictor variables, such as absolute body mass (which also includes aspects of body size), residual body mass controlling for tarsus length (body condition), and relative body mass (centered on individual mean values). The effect of sex was only assessed for breeders because only one of the immigrants was male and none of the related subordinates were female and thus no meaningful comparisons could be made. The effect of sex also differed between the variance response categories, and so a normal (not ordered) multinomial model had to be used in this case. As stated above, we used only the choice of the first tube that a bird opened after arriving at the feeder during each visit as the response variable to avoid problems of pseudoreplication. All models included only individual as random effect because neither group nor session number had any additional significant effects on the outcome of models. Estimation of the parameter values was carried out using a second-order penalized quasi-likelihood procedure (based on second-order Taylor expansions), and statistical significance of the explanatory variables was assessed by Wald tests (Rasbash et al. 2005).

## RESULTS

Breeders exhibited a preference for higher variances in reward size, whereas unrelated immigrant subordinate birds showed the opposite preference and tended to choose lower variance options (Figure 2a). This was confirmed by the ordered multinomial model (Table 1, Figure 2b) which revealed that unrelated immigrants had a significantly lower estimated probability of choosing the high-variance option and a significantly higher probability of choosing the no-variance option than did breeders. The choices exhibited by the few related subordinates in the sample did not differ significantly from those of their parents (Table 1) nor of the unrelated immigrants (Wald test: $\chi^2 = 1.388$, degrees of freedom [df] = 1, $P = 0.234$). There were also no significant differences between the choices of breeding males and females (Wald test: $\chi^2 = 1.381$, df = 1, $P = 0.240$).

Date and time had no effect on the choice of variance level (Wald test; date: $\chi^2 = 0.144$, df = 1, $P = 0.704$; time: $\chi^2 = 0.139$, df = 1, $P = 0.709$). There were also no differences between the choices made in the first 5 versus the subsequent 5 of the 10 data-collection sessions (Wald test: $\chi^2 = 0.196$, df = 1, $P = 0.658$), and all statistical models were therefore based on data from all 10 sessions combined.

Measures of body condition or state had no significant effect on foraging choices: neither body mass (Wald test: $\chi^2 = 0.129$, df = 1, $P = 0.719$), residuals of body mass controlling for tarsus length (Wald test: $\chi^2 = 0.232$, df = 1, $P = 0.630$), nor relative body mass centered on individual means (Wald test: $\chi^2 = 0.336$, df = 1, $P = 0.562$) were significant when included in the statistical model. Body mass also did not interact with social status (Wald tests: all $P$ values $>0.579$).

The inclusion of any of the factors excluded from the final model presented in Table 1 did not change the significance of the effect of social status on the probability of choosing

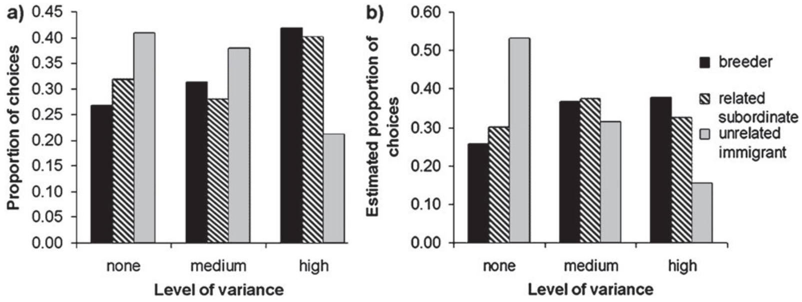

**Figure 2**
Bars represent (a) the total proportion of observed choices made by breeders (filled black), related subordinates (hatched), and unrelated immigrants (filled gray), for each of the 3 variance categories. (b) Bars represent the model estimates of the proportion of different choices made by the same classes of bird. The model estimates differ from the raw data in that they take into account that different individuals have been sampled unequal numbers of times.

different variance options (results not shown for reasons of brevity).

## DISCUSSION

Our results show that the birds in this study were variance sensitive and their variance preference depended on their social class: breeders were generally more variance prone, whereas unrelated immigrant subordinates were more variance averse. Given the design and large size of the feeders offering many different randomized food choices, and their visit-by-visit use by the birds, these results would appear to represent individual foraging decisions rather than any social interactions within group. These results may therefore be seen as support for the predictions made by McNamara et al. (1991), Bednekoff (1996), and Hurly (2003), where breeders are variance prone because they require additional energy to reach a further threshold for reproduction, whereas immigrant subordinates only need to reach a lower and more easily achieved survival threshold. In Siberian jay groups, the breeding pair are the only individuals to be involved in reproductive attempts and provisioning of offspring, and they also require more energy than immigrants as breeders are the primary individuals participating in defense of the group territory (personal observation, IIR).

The original energy budget rule suggests that variance-sensitive choices should be based on individual condition (Stephens 1981). However, we found no effects of condition, in terms of absolute body mass or mass relative to body size, on the foraging choices of jays. One reason for this could be that our study was performed during the autumn when there is no shortage of food and caching food in preparation for the winter becomes the main activity. In this system, the breeding season starts very early, before the snow cover disappears, and thus food cached during autumn is of great importance to individuals' subsequent breeding performance (Ekman et al. 1996). Therefore, we suggest that "state" in this variance-sensitive system is represented not by individual fat stores but by the size of the food hoard an individual has cached within the territory because this determines not only the probability of overwinter survival but, if it is a member of the breeding pair, also the further probability of successful reproduction (see Figure 3). Unfortunately, we could gather no meaningful data concerning the state (i.e., size) of individuals' food caches because they are cryptically scatter hoarded up in the trees. Therefore, for this system, we cannot make the comparison between the sizes of breeder versus subordinate food hoards or, more interestingly, compare the foraging decisions of individuals within each social class on the basis of their current food hoard size.

The lack of any effect of time of day further supports the notion that these birds were operating on the basis of long-term state of food stores, rather than any short-term (diurnal) variation in energetic state. There was also no evidence for a change in variance sensitivity of breeders over the season, which suggests that they do not acquire more than enough food for both surviving the winter and reproducing in the early spring, hence the suggestion in Figure 3 of a continuously rising utility function (i.e., no diminishing returns) for the highest state values.

Overwinter starvation is not common in our study population of Siberian jays (Griesser et al. 2006). This might explain why none of the immigrant individuals in the experiment exhibited variance-prone behavior, as they would be expected to if needing to reach the threshold of food hoard size required for survival. This does not mean that body condition is not likely to affect individual fitness through predation risk, either directly or through the risk-taking behavior necessary to

**Table 1**
**Predicted individual foraging choices**

| Parameters | Estimate | Standard error | Wald chi-square | df | *P* value |
|---|---|---|---|---|---|
| Intercept medium variance | 1.066 | 0.209 | 25.896 | 1 | <0.001 |
| Intercept high variance | −0.505 | 0.208 | 5.880 | 1 | 0.015 |
| Related subordinates versus breeders | −0.227 | 0.478 | 0.225 | 1 | 0.635 |
| Unrelated immigrants versus breeders | −1.195 | 0.333 | 12.902 | 1 | <0.001 |

Results of the ordered multinomial model of individual foraging choices where social class explains variation in choices. The intercepts are the cumulative logit of the probability that breeders choose this category or a category with higher variance. The estimated probabilities are shown in Figure 1b.

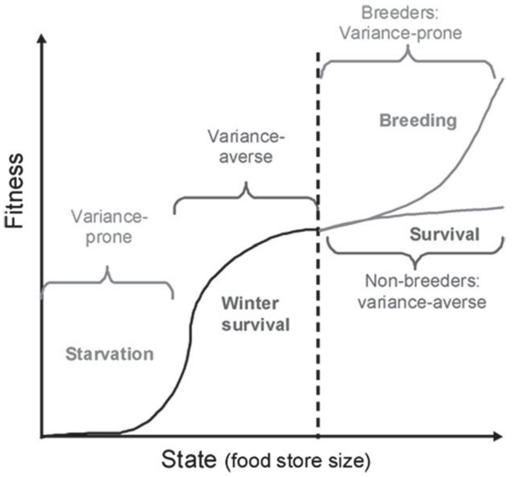

**Figure 3**
A graphical model of how variance sensitivity may relate to state (i.e., food store size) in Siberian jays. A utility curve (that relates fitness to state) of this shape may occur if starvation is likely when state is below a certain threshold, and breeding output increases continuously with state beyond a second higher threshold (dashed line). The black part of the utility curve is expected to be common to all birds in the population. In the regions where the utility curve is accelerating variance proneness in foraging is expected. Variance aversion is expected in the region where the curve is decelerating. The upper gray part of the curve is only expected to be relevant for the dominant breeding pair in each group as they are the only individuals that can take advantage of additional food stores for the purposes of breeding. Subdominant birds are not expected to have anything to gain by any additional increase in food store size beyond that required for survival, and so they are not expected to invest in increasing their state beyond the second threshold (dashed line), if they made such investment the utility curve for the subdominant birds would be expected to be decelerating (lower gray line).

obtain enough food for those individuals in lower condition. The most likely explanation for the differences in variance preference between the different social classes shown here appear to reflect the long-term effects of food hoard size and the additional reproduction threshold experienced by breeders but not subordinate immigrants. Because breeders have more to gain by gambling for higher rewards, a potential breeder might be expected to prefer higher variances than a nonbreeder, even when both individuals are in the same energetic state (Hurly 2003). Additionally, we would argue that immigrant food hoards were likely to be in a poorer state than those of breeders because of their lower dominance rank, poorer knowledge of the territory, and generally reduced access to food, and therefore would fall relatively further toward the left-hand side of Figure 3. Taken together, these arguments would explain why immigrant subordinates were variance averse, whereas breeders in our study population were variance prone. We could not detect whether retained offspring made different choices compared with breeders or unrelated immigrants, but this may have been due to low sample size given that data were only available for 3 such individuals.

Some of the only other studies of this type, on wild rufous hummingbirds (*Selasphorus rufus*), could be seen as lending support for the interpretation we are suggesting here (see Figure 3). All the individuals assessed in Hurly (2003) and Hurly and Oseen (1999) exhibited the same level of variance-sensitive preference, but it was for intermediate variance. The only logical adaptive explanation for this seems to be one that involves the existence of separate energetic thresholds for survival versus reproduction (Hurly 2003).

Previous studies have only occasionally found support for state-dependent variance sensitivity (reviewed in Bateson and Kacelnik 1998; Bateson 2002). However, most of these were on captive animals, which may therefore not have been able to perceive their state in a way that allowed them to make the adaptive choices predicted by theory. To our knowledge, the current study is the first to present results showing that wild birds in different states (i.e., social class) have contrasting variance preferences. A study of wild honeybees (*Apis mellifera*) is the only other example of individuals in different social situations showing differential variance sensitivity because workers were shown to be more variance averse than drones (Shafir et al. 2005). The explanation given was that drones are probably under less selection for variance sensitivity because they do not forage on flowers but are fed by the workers or feed from the relatively constant honey stores of the colony. This is in contrast to Siberian jays, where all individuals are expected to gain selective advantage from making the best choices in terms of the variance experienced in foraging rewards.

Such individual state-dependent foraging strategies are expected to have evolved through the use of relatively simple rules of thumb (Stephens and Krebs 1986), allowing animals to make rational choices in a complex natural environment. Variance sensitivity requires only that individual animals can assess their current state in terms of internal or (as in the case of food stores) external cues relative to their needs for survival and possible reproduction over a range of ecologically relevant timeframes. Such rules of thumb will, however, only work if they are employed in a similar enough environment with the same causal relationships to the one in which they evolved (Houston et al. 2007). We therefore cannot necessarily expect deliberately simplified laboratory environments and abstracted experimental protocols to provide a naturalistic enough set of cues to enable the animal to appropriately use such adaptive rules of thumb, especially if they involve anything more complex than individual short-term energetic state and survival over the next few hours. Indeed, the present study suggests that state-dependent foraging strategies such as variance sensitivity are likely to involve perceptions of alternative state variables perhaps operating over longer timescales. Such natural state variables are largely unrepresented within rarefied captive environments, and we would suggest that future studies should therefore be carried out under more realistic conditions in an attempt to include more ecologically relevant factors in state-dependent animal decision-making.

## CONCLUSIONS

Siberian jays appear to make variance-sensitive foraging choices, and these differ between social classes (breeders versus subordinate immigrants), presumably due to contrasting differences in state, differences in breeding opportunities (creating differing relationships between state and fitness in breeders versus subordinates), or a combination of the 2. The relevant "state" in Siberian jay autumn foraging proved not to be current body condition, but rather we suggest that it is food hoard size that will affect their chances of survival throughout the winter and, for breeders, their reproductive success in the following spring. This study therefore underlines the need for experiments of this type to be carried out under more natural conditions, in order to capture adaptive behavioral strategies based on the actual states that are being optimized over ecologically relevant timeframes.

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# paper II

# Private and public information use strategies by foraging groups of wild Siberian jays.

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## Abstract

In variable environments variance-sensitive foraging should be replaced by more profitable sampling behaviour whenever the variation in foraging rewards becomes predictable enough to track. We tested this suggestion in groups of wild Siberian jays (*Perisoreus infaustus*) during pre-winter food hoarding visits to experimental feeders of a type previously used to document variance sensitivity in this system. As predicted, all groups of jays switched to sampling once food items were clumped into ‘patches’ to create reliable patch-based information concerning prey sizes. However, increases in individual foraging success above chance were not achieved according to a simple ‘win-stay lose-shift’ rule of thumb. Instead jays employed a win-and-return-later strategy, returning more often over the experimental session to privately sampled patches containing the four largest of five prey sizes. In contrast, public information that was gained by observing patch sampling by other group members involved a more gradual increase in the probability of patch use with the prey size involved. Use of public versus private information did not differ according to sex or social status. Even though the jays did not achieve the individually optimal strategy in this specific experimental set-up, their sampling behaviour using both public and private information perhaps maximizes both individual and group-wide foraging efficiencies when exploiting the ephemeral food sources typical of boreal taiga forests.

**Keywords**: patch sampling, optimal foraging, stochastic environment, food hoarding, food storing

Animals rarely have perfect information about their foraging environment and therefore often benefit from sampling patches of uncertain quality. Sampling often carries an immediate cost in terms of reduced foraging efficiency because of the variable profitability of the patches sampled. This potential short-term cost of sampling must be balanced against the long-term benefit of such behaviour, i.e. when higher rewards can be gained from exploiting patches more efficiently based on the information obtained. If the long-term benefit of sampling is larger than the sum of the short-term costs, it is expected that animals will sample. In short, information is valuable when it can tell you something that changes your behaviour in a way that will increase your payoff (Gould 1974; Stephens 1989), and many studies of both captive and wild animals have provided evidence in support of sampling as a general phenomenon in foraging (e.g. Krebs et al. 1978; Lima 1984, 1985; Dow and Lea 1987; Tamm 1987; Shettleworth et al. 1988; Valone 1992; Valone and Giraldeau 1993; Templeton and Giraldeau 1996, Dall et al. 1997; Hall et al. 2007).

Animals have evolved to solve a variety of strategic problems, and to do so they are often assumed to use “rules of thumb” (McNamara and Houston 1980), which are behavioural approximations to the optimal solutions to problems. We expect that animals use such strategic simplifications instantiated as rules of thumb to optimize their sampling effort, because sampling is strategically complex but also important for the maximization of food intake rates. “Win-stay lose-shift” is a rule of thumb whereby an animal continues to exploit a resource if the reward is above some threshold (win-stay), but changes to a different resource if that threshold is not reached (lose-shift; Olton and Schlosberg 1978; Bicca-Marques 2005). Many studies demonstrate that animals are able to behave in a way that corresponds to the win-stay rule (Smith and Sweatman 1974; Bicca-Marques 2005 and references therein) or to the closely related “area-restricted search” strategy (e.g. Tinbergen et al. 1967; Smith 1974a,b) in which animals tend to keep searching for food in areas close to where they previously found food, often achieved by increasing the turning angle after prey capture. For the win-stay lose-shift rule to be an efficient approximation to the optimal solution, it is important that the information gained during a single sampling event is relatively reliable. A more complex rule of thumb for information use in foraging may involve Bayesian decision making (McNamara et al. 2006; Valone 2006) or other similar learning rules such as linear operator rules (e.g. Devenport and Devenport 1994; Gross et al. 2008). In such strategies, information from the most recent experience is given greater weight when combined in some way with previously gathered information (or starting estimates inherited from ancestors selected for their success in similar environments) to provide the best estimate of which patch or prey to choose. Therefore, learning-based rules, such as Bayesian updating and linear operator rules, can be powerful tools for animals to estimate the quality of a patch when a single sampling event does not provide reliable information and there are no rapid changes in the distribution of food.

All these strategies and rules of thumb involve animals generating “personal information” when they interact directly with their surroundings (Dall et al. 2005). However, animals can also acquire “public information” by observing the foraging success of other individuals and thereby gain useful information about the quality of a patch (Valone 1989; Valone & Templeton 2002). Public information can be beneficial if it reduces uncertainty about the quality of the environment and reduces the time needed to accurately estimate patch quality (Valone and Templeton 2002). Public information is considered a benefit of group foraging (Clark and Mangel 1984), but foraging in a group is costly not only because of competition, but also because accurate estimation of patch quality is harder when it is made more dynamic by foraging groups (Valone 1993). Thus public information is not only more available when in a group, but it may also become more important in order to gain good patch estimates during group foraging. The mix of personal and public information used should depend on the relative accuracy and costs of obtaining personal versus public information (Templeton and Giraldeau 1996; van Bergen et al. 2004).

In a system with options of unequal variance, animals are expected to prefer either the more or the less variable option depending on the shape of the relationship between the resource gained and fitness (e.g. Real and Caraco 1986; McNamara and Houston 1992). We have previously shown that Siberian jays (*Perisoreus infaustus*) in our study population are variance-sensitive (Ratikainen et al. 2010). Furthermore, we would expect that when the animals can gain any reliable information about the reward values of variable options, then variance sensitivity will be abandoned, and optimal sampling behaviour will take over (McNamara 1996). In our previous experiment there were three options providing the same mean return but with different variance, and no information about where the large rewards could be found (Ratikainen et al. 2010). In the current experiment we used the same three options again, but this time the sizes of rewards within each option were spatially clumped into patches within the feeder, allowing sampling to provide the birds with reliable information about reward size in the rest of a given patch. We therefore predicted that the jays would abandon any variance sensitivity and switch to pure sampling with the use of the additional information available in the new experimental set-up. The birds could obtain personal information about the different rewards from the combination of colour cues and spatial position during successive visits to the patches, and had to use this information appropriately in order to exploit the most profitable patches. In addition, we investigated the possible use of public information available from other group members visiting the feeding platforms.

## Methods

### *Study population*

This study included wild groups of Siberian jays (*Perisoreus infaustus*) living in boreal taiga forests close to Arvidsjaur in northern Sweden (65º 40`N, 19º 0`E). This species is highly territorial and lives in small groups centred around a breeding pair (Ekman et al. 1999). Some offspring disperse during their first year, and some disperse after several years (Ekman et al. 2002). Groups therefore consist of a mixture of the local pair, their retained offspring and subordinate immigrants (Ekman et al. 1994). The Siberian jay is an omnivore and eats insects, seeds, fungi, small mammals, carrion and berries (Andreev 1978; Borgos and Hogstad 2001). They gather food in autumn and store the individual items for the winter under tree bark and in lichen on the trees. This study was conducted during September 2008, when caching behaviour was ongoing. Siberian jays are rarely afraid of humans, making this an easy species to get close to and observe without disturbance. The population used here has also been habituated to humans over many years using supplementary foods (e.g. fat or sausage), and individually colour-banded, sexed and their status (as breeder, offspring or immigrant) determined as part of an ongoing study (see Ekman et al. 1994, 2000, 2002).

Of the eight groups of jays used in the current study, five groups contained five individuals, one group four individuals, one group three individuals, and one group only two individuals; in total 34 individuals participated in the experiment. All groups consisted of a mated pair, but in one of the territories the breeding male could not be identified, and thus all three males in this group were allocated ‘unknown’ status. In all except one group there were immigrant subordinates and in four cases also one or more retained offspring of the breeding pair.

*Experimental procedure*

During training and experimental sessions each group of jays was given access to a feeder placed horizontally on the forest floor in their territory. Each feeder consisted of 12 boards, sized 60x60 cm, and each board contained 12 plastic tubes sunken into the surface and organized in three patches (Figure 1). The feeder was therefore large enough for several birds to forage at the same time and they appeared to do so independently with little or no foraging competition or other direct social interactions. All tube lids were covered with opaque tape, and to see and obtain the sausage meat reward the birds first had to open the lid. A thin sheet of coloured rubber (green, black or purple) was also placed as a collar around each tube as a colour cue to the contents. Clusters of four tubes with the same colour were placed together to create a 'patch', with feeders containing twelve patches of each of the three colours (see Figure 1). All four tubes in a patch contained the same reward – i.e. the same size of sausage. Following Ratikainen et al. (2010), there were three types of food reward: no variance, moderate variance and high variance. The reward sizes in all the patches colour-coded as 'no variance' comprised 2.5 g in every tube in the patch. In patches colour-coded as 'moderate variance', half the patches consisted of four tubes each containing 1.75 g rewards and half of four tubes containing 3.25 g rewards. In patches colour-coded as 'high variance', half the patches consisted of four tubes where the reward was 1.0 g and the other half consisted of four tubes containing rewards of 4.0 g. Patches with variance contained no additional cue as to whether they contained the large or small pieces of sausage, and therefore the mean expected size of food reward was the same for all patches and colour-codes. The variance level associated with the different colour cues was randomised between groups, but kept constant throughout the experiment for a given group. No patches of the same colour were

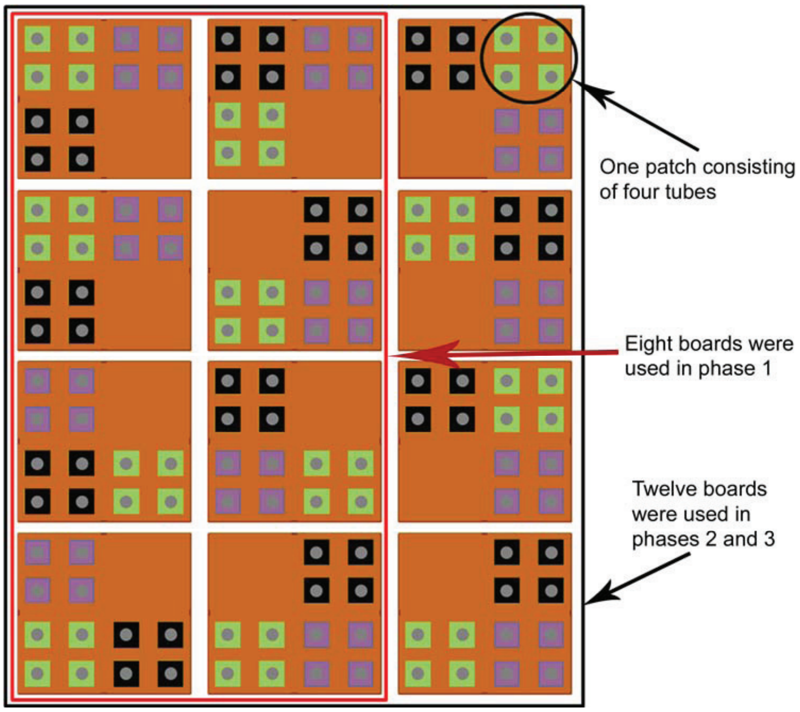

**Figure 1.** A schematic view of one feeder placed horizontally on the forest floor. Placement of patches here provides just one example of the random arrangement.

placed next to each other (see Figure 1); and the relative spatial positions of patch type and profitability were randomized between sessions.

Our experiment contained two levels of information: firstly there were three distinctly different foraging options with colour cues consistently indicating the variance associated with each option. All foraging options had the same expected mean reward associated with them and thus colour did not provide any information about which patch would be most profitable to exploit. We have previously shown that jays in this population use variance-sensitive foraging strategies when faced with colour cues to variance in (but not mean) rewards from different foraging options (Ratikainen et al. 2010). The second level of information lay in the spatial positioning of foraging options in patches, with all rewards being identical within the same patch. Therefore, having exploited any part of a patch, the birds had reliable information about the profitability of all other tubes within that patch. However, for the foraging options involving variance, the spatial arrangement of patches of small versus large reward changed between experimental sessions, and birds were therefore always required to sample a patch to acquire information about its relative quality in any one session.

The birds were trained to take very small pieces of sausage from a top ban balance, and whenever possible body mass was obtained for all individuals within a maximum time of 10 minutes before the start of each session with the experimental feeder. All training and experimental sessions were video-taped from a distance of 3-4 metres between the feeder and camera (Panasonic NV-MX500). All sessions were simultaneously observed directly from a distance of 4-5m and individual bird identity was noted per visit to the feeder, using binoculars with a verbal commentary recorded on the video soundtrack.

Before the start of the first training sessions, birds were taught how to open the feeder lids by first leaving the lids of all tubes only half closed, then in the next session closing them only very lightly, and then gradually closing the lids more and more tightly over time, thus requiring the birds to actively open them. The experiment then progressed through three phases. The first phase consisted of five training sessions, in which only eight boards were used (see Figure 1). These sessions were terminated once the boards were completely depleted, or after a maximum of 1 hour, whichever occurred first. This allowed the birds to gain experience with all the patch types and their associated rewards. The second phase consisted of five training sessions using all 12 boards in the feeder (see Figure 1). These sessions were terminated after 30 minutes or when all the tubes of one colour had been opened. The purpose was for the birds to further learn the rewards and that sessions ended before all the tubes were opened, and therefore that the sequence of patch use was important in order to maximize individual rewards. The third and final phase involved five experimental sessions in which data were collected. In these sessions, 12 boards were used and sessions were ended after 30 minutes or once all the tubes of one colour were opened, as in the second phase. Therefore, this again required birds to maximize the overall rewards gained via prudent patch choice.

The videotapes from the five experimental sessions per group were later analysed to score all individual choices. All birds in all groups flew back up into nearby trees to store nearly all the food items obtained. The mean±std. dev. number of visits to the feeder for each bird per session was 13.06±6.32 (range: 1-38). Each bird opened on average 1.42±0.70 (range: 1-6) tubes during a single visit to the feeder. For every visit, both individual identity and the patch of all tubes opened were recorded, along with the size of the rewards gained from the patch and the distance of the patch from the observer, measured as row number from one to eight from closest to observer to furthest respectively. In cases where more than one tube was opened during a single visit to the feeder, the order of the tubes opened was also recorded.

*Statistical methods*

As successive patch choices may be non-independent (due to spatial proximity), only the first tube a bird opened after it had arrived at the feeder was used in the analyses. In a small minority of instances, involving 73 of 3422 (2.13%) cases where a bird opened a lid, it was difficult to identify which individual was involved. As it was important to know each bird's previous choice, the data from visits by unknown birds were therefore excluded from any statistical analysis. In addition, in a few cases (33 in addition to the 3422 tubes opened) the focal individual ate the sausage from a tube that another individual had opened; the information the focal bird acquired from this was included, but it was not counted as a choice. In three sessions, two patches of the same colour were placed beside each other due to an error in setting up the feeders. In two of these cases, the patches next to each other contained the same food reward size and were therefore treated as a single 'patch'. In the third case, the patches contained different reward sizes and these data were therefore removed from the analysis.

To compare the foraging success of individual birds against expectations from theory, a simple model was created to simulate the rewards from a perfect win-stay lose-shift strategy in the experimental set-up we used. A non-spatial representation of the 36 patches each containing four equal rewards was assigned reward sizes as in the experiment (see above). One to five individuals were simulated and allowed to remember the success of the last patch they visited and all the patches with rewards that were smaller than a given threshold (threshold values applied were 1.0 g and 3.25 g). In this simulation, a group size of one corresponds to perfect social information, as in a scenario where all birds have all the information of all other birds. For a given number of visits to the feeder by the group as a whole (see below), the following procedure was repeated: on a given visit a single random individual in the group was picked, if the previous patch that individual had visited was a patch with a 'large' reward (larger than the set threshold), and the patch was not empty, the individual visited the same patch again (win-stay). If the previous patch contained a 'small' reward (threshold or lower) the previous patch was avoided for the rest of the "experiment" if possible (lose-shift). The rewards obtained and the individual birds were recorded for all visits in each simulation run. For each of the number of visits to the feeder by the group as a whole (varied from 30 to 140, in intervals of 10), the simulation was repeated 10 000 times. For each individual, the mean reward size obtained was then calculated across the 10 000 simulations of a given run length.

To test how the wild birds in the experiment used the information available to them, logistic regression models were applied. Firstly, to test for the use of a win-stay lose-shift strategy, an immediate return to the same patch as previous (stay) or a switch to a different patch from the previous (shift) was tested against the previous reward size. We did not include data points when a patch was emptied before the same bird revisited the feeder. Secondly, we tested for an alternative longer-term version of the win-stay lose-shift strategy in which individuals might return with a higher probability to patches that provide large reward sizes, and crucially this return did not have to take place during the next visit but could occur on any subsequent visit during the same session. Finally, we tested if a bird's probability of visiting patches previously opened by other members of the group was affected by the size of the reward in that patch. For this analysis we excluded all data where an individual returned to a patch it had already visited before itself, because we were interested in checking specifically for the use of public information.

Because of the experimental procedure, the random probability of returning to a patch alters as more patches are sampled and other patches are emptied. We therefore included an offset term in our logistic regression to account for this. The offset term was: $\log(p/(1-p))$, where p was the random probability of returning to a previously visited patch, calculated for each visit. P was calculated slightly differently in the three different models. The random probability of immediately returning to a patch was: $p=1/(t-e_t)$, the random probability of returning to a patch previously visited by the focal individual itself was: $p=(s_f-e_s)/(t-e_t)$, while the random probability of visiting a patch previously visited by another group member was: $p=(s_g-e_t)/(t-e_t)$. Where $s_f$ is the number of patches sampled by the focal individual, $s_g$ is the number of patches sampled by the group, $e_s$ is the number of the sampled patches that has been emptied, t is the total number of patches, and $e_t$ is the total number of empty patches. In Figures 3 and 4, the null model is included as a line of random expectation; this line is calculated from model estimates of a linear regression of distance from observer. This was used only for graphical representation and not for any statistical comparisons.

In addition to patch quality (reward size), the probability of returning to a profitable patch or avoiding an unprofitable patch was tested in all these models against: social status, sex, group size, distance from observer (i.e. position on the feeder), the choice (tube) number within the experimental session and the interaction between reward size and each of the other explanatory variables. Group size included in the analysis included all birds that visited the feeder in the relevant session, in a few cases that included a few extra birds from a neighbouring territory in addition to the residential birds. Evaluation of these fixed effects was based on sequential removal of variables with subsequent ANOVA comparisons until log-likelihoods (based on Maximum Likelihood, ML) decreased significantly (see Zuur et al. 2009). As a final step, the additional explanatory variable of body mass was added to the most parsimonious model selected by this procedure, and this was tested by a further ANOVA comparison. The models compared were both estimated based on a restricted dataset, because we did not have the body mass for all individuals in all sessions. Whenever we found that the reward size affected the probability of returning to a patch, we checked if this was due to within- and/or between-subjects effects, as described in van de Pol & Wright (2009).

To control for non-independent observations within individuals and groups, these were fitted as nested random factors (individual nested within group) in all mixed effects models. R Version 2.13.0 (R Development Core Team 2011) was used throughout. For the mixed models, the *lmer* function in the *lme4* package (Bates & Maechler 2009) was used with ML estimation procedure for model selection, while REML was used to obtain more accurate parameter estimates for the final version of each model. A significance value of 0.05 and two-tailed tests were applied throughout.

## Results

### *Success when birds visit a new patch*

As intended, the birds showed no knowledge of which patch contained large versus small sausage items when they had only pre-harvest information. Birds received a mean reward of size 2.511±0.033 g from the tubes opened in a patch that they had not exploited before. This reward size is not significantly different from 2.5 g (Wilcoxon signed rank test: p=0.717, N=882), which would be expected from a random choice of tubes.

### *Overall success in exploiting profitable patches*

In the 2431 valid visits to the feeder, the birds obtained rewards of mean size 2.603±0.020 g. This was significantly larger than the mean size 2.5 g available overall (Wilcoxon signed rank test: p<0.001, N=2431). Therefore, birds must have obtained and used some form of information to improve their performance above that expected by chance.

The results of the model simulating a simple win-stay lose-shift response to the experimental set-up (Fig. 2) show that the mean reward size obtained should be dependent upon the running total number of visits to the feeder by the group within a session. The simulation also showed small differences in mean reward size for different group sizes, such that individuals in large groups should have found on average smaller rewards when compared with individuals in smaller groups. However, these group size effects were not reflected in the data, and so for simplicity the lines in Figure 2 reflect the average predictions across all group sizes. Figure 2 also shows the mean number of visits to the feeder by each of the different groups during their experimental sessions and the mean reward sizes obtained. Given the results of the simulation for these numbers of visits to the feeder, we would not expect the mean reward size obtained by the birds to be any larger than approximately 2.8 g (Fig. 2), if they had used a perfect win-stay lose-shift strategy.

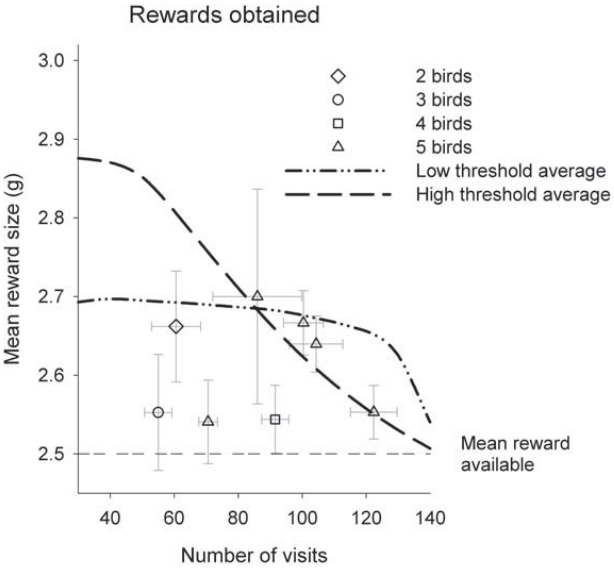

**Figure 2.** Mean reward sizes versus total number of successive visits to the feeder by the whole group, as predicted from the simulation model of a perfect win-stay lose-shift rule of thumb (see text for details). The two lines represent two different threshold values individuals use to evaluate if a reward is a "win" or a "loss". The dotted line represents how the mean reward size changes over time if the threshold value is low (1.0 g) and the dashed line represents the same for a high threshold value (3.25 g). The eight points in the background show the actual mean (±SE) rewards obtained by each of the experimental groups given the mean number (±SE) of tubes opened by the respective group during the experimental sessions (i.e. tubes opened is equated to number of visits in the simulations on the x-axis), with the different symbols indicating the group size in each

### *Testing for a win-stay lose-shift strategy*

The model selection shows that the model best describing the probability of immediately returning to a patch was not affected by any of the tested variables, and the null model with only the intercept was the final model. Reward size was not included in the most parsimonious model. In addition, none of the other explanatory variables (status, sex, group size, body mass, distance from observer, number of tubes opened in the session or the interaction between reward size and any of the other variables tested) were included in the most parsimonious model after model selection. From this, and the lack of a match to the simulation model (Fig. 2), it therefore seems that the birds were not following a simple win-stay lose-shift strategy.

### *Return to a patch visited previously in the same session*

Despite the lack of a strict win-stay lose-shift strategy, within any experimental session as a whole the birds were significantly more likely to return to patches from which they had previously obtained larger rewards (Table 1; Fig. 3). There was a significant difference only between rewards of 1.0 g and all other reward sizes (1.75 g, 2.50 g, 3.25 g and 4.0 g). This was essentially restricted to a within-subjects effect (slope: 0.087±0.036, p=0.016), rather than between-subjects (slope: 0.284±0.436, p=0.515). This indicates that the effect was not due to certain individuals consistently obtaining larger rewards and also exhibiting a generally higher tendency of returning to the same patches. Rather, the effect was due to all individuals adjusting their behaviour to the different reward sizes in similar ways. The estimated tendency to return to a patch was higher than that expected from a random choice of patch (see Fig. 3). The probability of individuals returning to a patch during a given experimental session was also affected by the distance of the patch from the observer – i.e. patches further away and closer to the trees and perches used prior to landing on the feeder surface were exploited first within any one session. Other explanatory variables tested (group size, status, sex, body mass, tube number within session, interactions between reward size and any of the other explanatory variables tested) were not included in the most parsimonious model, suggesting no significant effect of these factors on the probability of returning to a patch during the session.

**Table 1** Effects of pairwise comparisons of reward sizes on the probability of returning to a patch previously visited during the session. Results shown are from the final reduced logistic regression model (based upon 2183 visits). Significant p-values are shown in bold (see Fig. 3).

| | Effect size | SE | p-value |
|---|---|---|---|
| Intercept (reward 1.00 g) | 0.493 | 0.162 | **0.002** |
| Reward 1.75 g vs. 1.00 g | 0.513 | 0.187 | **0.006** |
| Reward 2.50 g vs. 1.00 g | 0.581 | 0.165 | **<0.001** |
| Reward 3.25 g vs. 1.00 g | 0.630 | 0.182 | **0.001** |
| Reward 4.00 g vs. 1.00 g | 0.638 | 0.178 | **<0.001** |
| Distance from observer | 0.154 | 0.023 | **<0.001** |
| Reward 1.75 g vs. 2.50 g | | | 0.658 |
| Reward 1.75 g vs. 3.25 g | | | 0.487 |
| Reward 1.75 g vs. 4.00 g | | | 0.454 |
| Reward 2.50 g vs. 3.25 g | | | 0.736 |
| Reward 2.50 g vs. 4.00 g | | | 0.685 |
| Reward 3.25 g vs. 4.00 g | | | 0.959 |

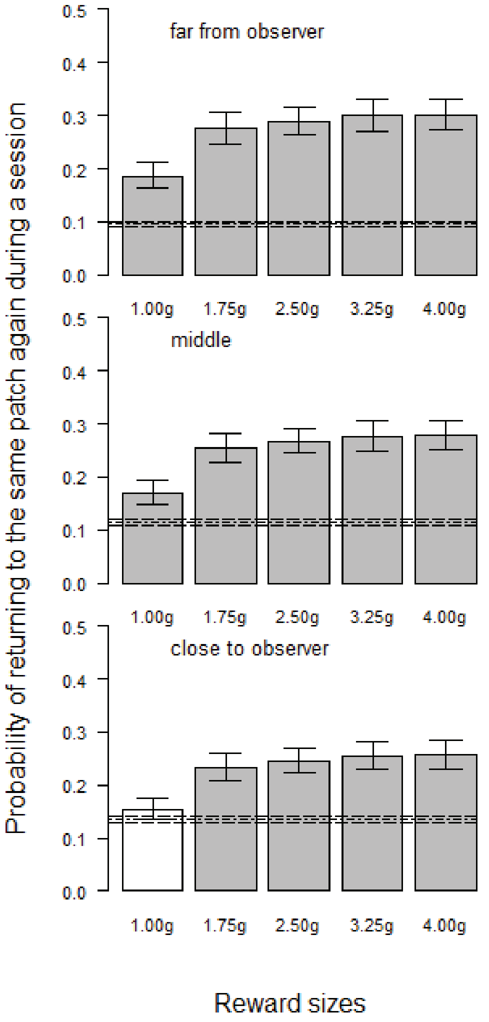

**Figure 3.** Estimated probability (±SE) of returning to the same patch again during a session according to the size of reward. Filled columns indicate a significant difference (win-return or lose-avoid) from random choice, showing a win-return pattern for all but the 1.0 g rewards (see Table 1). The dashed line indicates the average probability (±SE) of visiting a non-empty patch based upon random choice. As distance from observer had a positive effect on the probability of returning to a patch, the estimated probabilities are shown for three distances (from top to bottom); far from observer (distance 7/8), middle (distance 5/8) and close to observer (distance 3/8).

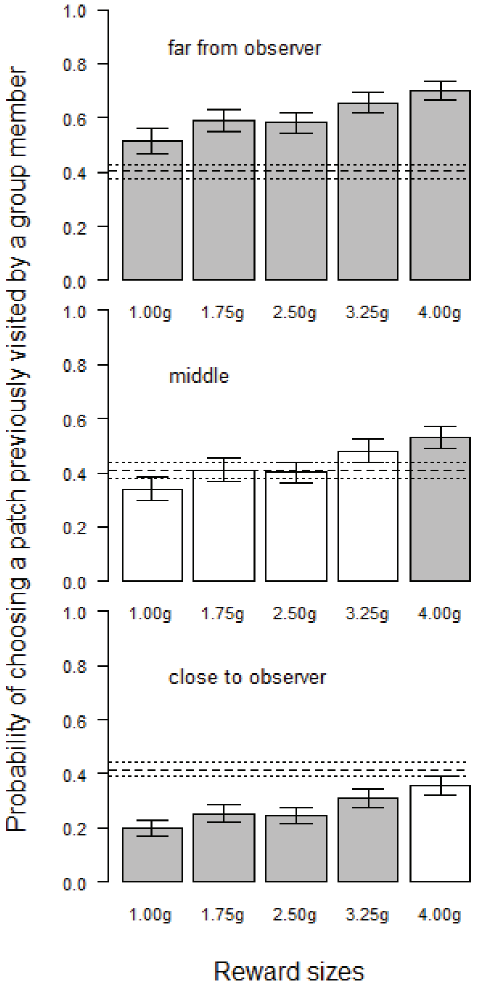

**Figure 4.** Estimated probability (±SE) of choosing a patch that has only been visited by another group member and not by the focal individual itself at the mid-session choice point (choice number 40; see Table 2). Filled columns indicate a significant difference (win-return or lose-avoid) from random choice. The dashed line indicates the average probability (±SE) of visiting a non-empty patch based upon random choice. As distance from observer had a positive effect on the probability of returning to a patch, the estimated probabilities are shown for three distances (from top to bottom); far from observer (distance 7/8), middle (distance 5/8) and close to observer (distance 3/8). Note the different scale on the y-axis compared with Fig. 3.

### *Use of public information*

To test whether the birds were also using public information, we investigated the mean reward size each bird obtained when opening a tube in a patch they had not previously visited themselves, but where another group member had already opened at least one tube. In comparison to the mean reward size of 2.511 g for completely untouched patches (above), a mean reward of 2.620±0.034 g was obtained on average by the birds in patches already visited by another group member. This was significantly higher than 2.5 g (Wilcoxon signed rank test: $p<0.001$, N=812), suggesting that some form of public information was being used.

Within each session as a whole, individuals were significantly more likely to open tubes in patches where other birds had previously found large rewards (Table 2; Fig. 4), even if they had never visited that patch before themselves. Individuals were also even more likely to open tubes in patches that other individuals had already sampled when they were far from the observer and it was late in the session (Table 2; Fig. 4). Other explanatory variables tested (group size, sex, status, body mass, and interactions between reward size and any of the other covariates) did not have any effect on the probability of returning to a patch during the complete session (i.e. were not included in the most parsimonious model chosen by model selection). As with the private information (above), this effect of reward size on the probability of opening a tube in a patch was due to a within-subjects (slope: 0.115±0.030, $p=0.003$) rather than between-subjects effect (slope: -0.497±0.456, $p=0.276$).

**Table 2** Effects of pairwise comparisons of reward size on probability of returning to a patch previously visited by another group member (but not the focal individual), during the session. Results shown are from the final reduced logistic regression model (based upon 1625 visits). Significant p-values are shown in bold (see Fig. 4).

| | Effect size | SE | p-value |
|---|---|---|---|
| Intercept (reward 1.00 g) | -0.683 | 0.207 | **0.001** |
| Reward 1.75 g vs. 1.00 g | 0.298 | 0.206 | 0.148 |
| Reward 2.50 g vs. 1.00 g | 0.265 | 0.180 | 0.141 |
| Reward 3.25 g vs. 1.00 g | 0.580 | 0.204 | **0.005** |
| Reward 4.00 g vs. 1.00 g | 0.794 | 0.200 | **<0.001** |
| Distance from observer | 0.378 | 0.032 | **<0.001** |
| Choice number within session | 0.012 | 0.003 | **<0.001** |
| Reward 1.75 g vs. 2.50 g | | | 0.852 |
| Reward 1.75 g vs. 3.25 g | | | 0.162 |
| Reward 1.75 g vs. 4.00 g | | | **0.013** |
| Reward 2.50 g vs. 3.25 g | | | 0.076 |
| Reward 2.50 g vs. 4.00 g | | | **0.002** |
| Reward 3.25 g vs. 4.00 g | | | 0.278 |

## Discussion

Our results clearly show that Siberian jays are able to use both private and public sampling information to increase their foraging success beyond what might be achieved by random choice alone. Moreover, this was achieved within a realistically complex foraging scenario analogous to one in which these birds have been shown to employ variance-sensitive foraging strategies (Ratikainen et al. 2010). Therefore, we were able to confirm the conceptual link that we suggest exists between sampling and variance-sensitive foraging strategies, the use of which should depend upon the relative amount of stochasticity that foragers experience. Unpredictable variability in foraging rewards should be met with variance-sensitive responses, but these are replaced by sampling behaviour whenever reliable information is available concerning predictable variation in foraging returns in order to adaptively track this variation. The results presented here confirm these predictions, causing the birds to abandon any variance sensitivity in favour of sampling, by introducing only a small amount of reliable information into an otherwise stochastic experimental scenario. Interestingly, the differences in variance sensitivity previously recorded between different classes of Siberian jays within groups (Ratikainen et al. 2010) were not reflected in the sampling behaviours recorded here. All classes of bird appeared to sample and to use public versus private information to a similar degree.

Comparing the jays' experimental performance against the results of the simulation model revealed that the mean foraging success achieved by the birds was above that expected by chance. However, it was also only about half as much above random performance as could have been gained via the use of a perfect win-stay lose-shift strategy, based exclusively upon private information. This mismatch was in accord with the finding that win-stay lose-shift was not the strategy being employed by the jays in this case. Rather than immediately returning to better quality patches, all birds seemed to apply a strategy based on information gained throughout the course of the experimental session, by revisiting patches containing the large sausage rewards at a higher probability than other patches.

In addition to the effect of reward size on the probability of returning to a patch there was also a positive effect of distance from the observer, which in most cases was also the inverse of distance from cover and the trees used to cache items and perches used to access the feeder. This was because the observer with the video camera had to be positioned in a direction with little cover in order to be able to observe the feeder. It has been shown previously in this population that the jays prefer to forage close to cover (Nystrand 2007). It is therefore not possible to ascertain whether the effect we find is due to an anti-predator preference to forage far from the observer and close to cover (e.g. Lima and Dill 1990), or if it is due to a preference to reduce travel costs and forage close to routes used to travel to and from local cache locations.

The performance of any animal in an artificial foraging task depends upon both its previous experience and the environment in which its ancestors evolved. The optimal behaviour in natural foraging situations may be approximated by simple rules of thumb, but these may not function as effectively if the animal is outside the environment in which it evolved (McNamara and Houston 1980; Houston and McNamara 1999). The complete reliability of information in this experiment meant that a simple win-stay lose-shift strategy would have outperformed any other strategy. However, the jays' strategy of returning more often to larger reward patches when an entire session is considered seemed to be closer to a learning rule such as Bayesian patch estimation or a linear operator rule. The advantages of such a rule of thumb would include fewer errors in patch choice due to inaccurate information from single sampling events (McNamara et al. 2006). This kind of cautious information use has long been seen in artificial feeder experiments, such as a persistent return to the locations of previously good patches long after they have been experimentally switched into being consistently poor patches (Smith & Dawkins 1971). Empirical studies of several different species now provide more direct evidence of specifically Bayesian foraging, notably in experimental situations that correspond well to patterns that would result from Bayesian-like updating of information in Argentine ants, *Lasius humile* (Nonacs and Soriano 1998), degus, *Octodon degus,* (Vasquez et al. 2006) and budgerigars, *Melopsittacus undulatus* (Valone and Giraldeau 1993).

Learning rules such as Bayesian updating were clearly inappropriate as a strategy to exploit our feeders, because a single sampling event in one patch provided perfect information about that patch. However, the existence of such rules of thumb might well reflect adaptive responses to the uncertainty around information gathered by sampling in the jays' natural foraging environment, where patch dynamics are likely to be more complex, and information from only one sampling event would not be as accurate as in our experimental situation. The Siberian jay is known to forage on many different sorts of food, including berries, insects, fungi, small mammals and carrion (Andreev 1978; Borgos and Hogstad 2001). The distribution of these in space and time is likely to vary between food types, and the predictability within any type may also be variable. Carrion, at one extreme, is very unpredictable in where and when it can be found, but is probably conspicuous to the jays and as soon as it is localised is likely to be a very good resource for as long as it lasts (until it is eaten by any larger animal). In a situation like that, a simple win-stay strategy might be expected. Berries, at the other extreme, are likely to be found in the same areas time after time, but the quality of a patch of berries may vary in both time and space, and be less conspicuous to the jays, and therefore require more sampling to determine its quality relative to other available food sources. Choosing the unknown may result in reward and always provides information while choosing the known only results in reward (McNamara and Houston 1980). The between patch foraging decision in this experiment probably resembles the berry scenario more closely because although the food was found in the same general place every time (i.e. the feeder), it was hidden and patch quality varied in both time and space according to featural (colour) cues. The jays might therefore have been employing a strategy that would have performed well under natural foraging conditions of this type, even if it was not the best strategy in our specific experimental design.

We have previously demonstrated the value of carrying out foraging experiments in the animals' natural environment, especially when exploring state-dependent strategies such as variance sensitivity (Ratikainen et al. 2010). However, this then exposes the hidden assumptions behind many experimental investigations concerning the cognitive processes and behavioural rules of thumb the animals are expected to employ in completing what amount to highly artificial foraging tasks (see Sulikowski et al. submitted). Laboratory experiments usually involve sufficiently long training periods that the task is in fact testing an individual's ability to learn a completely novel foraging problem, and these studies therefore assess the potential capabilities of a species. Foraging experiments in the wild cannot do the same, and in contrast rely more upon naturally evolved processes being implemented to solve a closely controlled artificial task. Care therefore needs to be taken to tailor the experimental task to natural foraging behaviours in order to properly explore what has evolved and perhaps to find out why. In the current study, we presented a relatively complex foraging task to wild Siberian jays, but to a large extent it replicated a natural foraging situation and allowed us to answer the questions we were interested in. However, in order to fully understand the foraging strategy we have observed, we now need to explore the precise rule of thumb being used when the jays assess the changing value of a patch. As the discussion above suggests, this requires some appreciation of the natural foraging tasks jays have evolved to perform, but mostly an experimental scenario that manipulates the flow of private and public information available to the birds.

Public information may be less accurate than private information (e.g. due to sensory limitations), and in our study there was a trade-off between time spent watching group members and caching food, i.e. a time cost of public information gain. These costs, in addition to less precise patch estimates due to group effects, may be countered by the benefit of additional information obtained from group members (Valone 1993). Our results support previous studies (Templeton & Giraldeau 1995, 1996; Smith et al. 1999) in clearly showing that the use of public information increases individual pay-offs in foraging. As with the use of private information, there did not appear to be any effect of group size or any patterns in the use of public information, and we could not demonstrate any differences between classes in their use of public information. Use of public information therefore allowed all individuals to benefit from foraging as part of a social group, perhaps at the cost of reducing further the value of the private sampling information gathered within larger groups. Such group-wide increases in foraging efficiency would benefit individuals if natural foraging opportunities on discrete food sources are time-limited, for example, due to the end of daylight or interruptions at food sources (e.g. carrion) by predators or other more dominant species of birds or mammals.

Interestingly, public information seemed to be used somewhat differently from privately acquired information (compare Figs. 3 versus 4). The use of private information showed a distinct threshold; the smallest prey items were returned to only as often as would be expected from random patch choice, whereas a general win-return at some future point in the session was used for all other larger reward sizes (Fig. 3). In contrast, there was a more continuous positive effect of reward size in the use of public sampling information. Individuals were increasingly likely to visit a patch that they had not sampled before themselves, the greater the prey size that had been obtained at that patch by another group member (Fig. 4). It is not easy to provide a clear explanation of this difference between the use of private and public information, but we can speculate based on the general differences between the two types of information. It is relatively safe to assume that it is harder to estimate the sizes of rewards found by other individuals compared to the ones found by oneself. Public information may therefore be less accurate than private information in this experiment, and the jays may have been unable to employ the same strategy when using public information as when using private information. This is not sufficient to completely account for the difference though. It is not only the patches with the smallest sausage sizes that are visited less than patches with the largest rewards when public information is used, there is a gradual response to increasing reward size, and this would not be expected if it was purely a perceptual error. The difference may of course also arise because of some unknown aspect of how the jays use information on different types of food items under natural foraging conditions. Again, this underlines the points made above concerning the hidden assumptions implicit in the design of artificial foraging experiments. This is because we cannot be sure that we have presented the problem in a cognitively recognisable format for the species concerned and the foraging tasks it has evolved to solve (see Sulikowski et al. submitted).

In summary, using an artificial foraging task with wild Siberian jays we were able to confirm the important conceptual link between variance sensitivity and sampling behaviour, because the jays switched to sampling (environment tracking) once reliable information was made available in an experimental scenario previously shown to elicit only variance-sensitive responses (Ratikainen et al. 2010). However, the sampling strategy used by the jays did not fully exploit the high reliability of the information provided by the experimental feeders. This may reflect the uncertainty around the information concerning natural food types, suggesting that jays have been selected to use more complex sampling rules of thumb more akin to

Bayesian updating rather than a simple win-stay lose-shift. Both public and private information were used, irrespective of individual sex or social status. This is what can be expected in groups that rapidly exploit ephemeral food sources in the boreal taiga forest environment because of the high need for accurate information in such situations.

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# paper III

# Use (and mis-use) of configural versus featural cues by a caching corvid, an omnivorous honeyeater and an innovative parrot

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## Abstract

Numerous studies have compared animal use of featural cues (colour, shape) and configural cues (relative spatial relationships) while foraging. A tendency to rely on configural cues more than featural cues has been hypothesised to be an adaptation to food caching and recovery, being observed in some food-storing birds, but not in closely related non-storing species. A thorough review of the literature, however, reveals little evidence for a simple preference for configural over featural cues in predominantly storing species. The current study presents data from Siberian jays, noisy miners and kea parrots on three tasks, which placed featural and configural cues in conflict. Both jays and miners preferred to use the configural cues, while the kea preferred to use the featural cues. Miners and kea also showed a capacity to use their non-preferred cue type when the preferred cue was unavailable, whilst jays have already been demonstrated to possess this capacity. Our findings therefore show no clear pattern with respect to foraging ecology in these three quite dissimilar species: Siberian jays are generalist food-storers, noisy miners are nectarivorous and also forage for cryptic insect prey and kea are innovative foragers that routinely exploit novel food sources. There appears to be no general relationship between ecology and the use of featural versus configural cues. Instead, we suggest several hypotheses for further investigation, and recommend that greater consideration is taken of potential interactions between species ecology and the demands of the specific task being presented.

## Keywords

spatial cognition, foraging ecology, featural and configural cues, *Perisoreus infaustus*, *Manorina melanocephala*, *Nestor notabilis*

Where to search for food is a ubiquitous problem facing most mobile animals. Trying to understand how animals make this decision, particularly with respect to information available to the animal during previous successful and unsuccessful foraging attempts, has yielded a wealth of research into small-scale spatial cognition. A variety of ecologically varied groups have been investigated, including rats (Cheng and Newcombe 2005), pigeons (Cheng et al. 2006), nectarivorous birds (Hurly and Healy 1996) and bats (Carter et al. 2010), and food-storing birds and rodents (Smulders et al. 2010). Of most relevance to the present research are studies that have compared animal use of featural cues (such as the colour, shape or size of an object) with their use of configural cues (that is the spatial configuration of landmarks or the absolute or relative position of a goal).

The differential use of featural versus configural cues during small-scale foraging has been investigated extensively using both food-storing and non-storing bird species. As might be expected, several studies on food-storing and non-storing Corvid species have shown that food-storing species have better spatial-cognitive abilities than non-storing relatives (Balda and Kamil 1989; Bednekoff et al. 1997; Kamil et al. 1994; Olson 1991). However, similar research on Parid species has been less conclusive (Clayton and Krebs 1994a; Healy 1995; Healy and Krebs 1992). Storing, but not closely related non-storing, Parid species respond preferentially to spatial versus colour cues when both are presented as one-trial memory tasks (Brodbeck 1994, Clayton and Krebs 1994b), with similar findings reported using operant delayed match to sample tasks (Brodbeck and Shettleworth 1995). A preference for global spatial cues over local shape and colour cues has also been demonstrated (Herz et al. 1994). These findings have in general been interpreted as indicating that preferential use of spatial over colour information is associated with food-storing behaviour and may represent an adaptive specialisation of cognition that results in enhanced cache-recovery. This hypothesis leads to the prediction that food-storing species should show a preference to attend to configural over featural information, but non-storing species should show no such preference. Consistent with this notion, some non-storing species, such as great apes (Kanngiesser and Call 2010) have shown a preference for use of shape and colour compound cues over spatial information, while another study suggested that pigeons have no preference for either a shape and colour compound cue over spatial information when the two are placed in conflict (Reynolds 1961).

Some more recent findings, however, on both food-storing and non-storing species suggest that current evidence does not support the notion of a simple association between food-storing behaviour and a preference for configural cues. For example, not all food-storing species exhibit a preference for configural over featural cues in experimental tasks. LaDage and colleagues (2009) showed that food-storing mountain chickadees, preferred a colour cue over a relative spatial location cue, when relocating a conditioned feeder, as long as the colour cue was less complex than the spatial cue. Pravosudov and colleagues (2005) found no clear preference for either colour or spatial cues in food-storing western scrub-jays during a short-delay memory task. Waisman and Jacobs (2008) showed that free-ranging fox squirrels, a food-storing rodent, showed a preference for a colour and shape compound cue over spatial cues when the two were placed in conflict (although the reverse preference was shown when the colour/shape cue was made more complex); while food-storing flying squirrels tended to rely on both spatial and colour cues, averaging the two when they were placed in conflict (Gibbs et al. 2007).

Conversely, some non-storing species have shown a preference for configural over featural cues. Hodgson and Healy (2005) report a preference for a relative spatial cue over colour cues in the non-storing great tit, although the same species previously failed to show this preference when tested by Clayton and Krebs (1994a). With respect to nectarivorous species, both flower bats and fruit bats preferentially use location cues over olfactory cues (Carter et al. 2010) and bumblebees (Ney-Nifle et al. 2001) and free-flying hummingbirds (Healy and Hurly 1996) also seem to prefer configural to featural cues, electing to return to a previously rewarded location rather than to a feeder of a previously rewarded colour. Wild hummingbirds also return to within 70cm of a location where an artificial flower used to be, before apparently noticing it had been removed or shifted (Hurley et al. 2010).

As well as the rather inconsistent association between food-storing tendency and cue preference, there is also evidence that the notion of simple preferences for one cue type over another does not adequately describe observed patterns of cue use. For example, Humber and colleagues (2009) report that pine siskins, a non-storing granivorous bird, visit backyard feeders based on their relative location to each other rather than their colour. When the order of colours in a row of feeders was reversed, however, the birds' visitation rates followed the colours, suggesting that the birds used the colour cues to orient themselves correctly to the feeder configuration. Such facilitation of spatial learning by visual pattern cues has also been demonstrated in humans (Sturz et al. 2010). Thiele and Winter (2005) demonstrated that flower bats initially choose to revisit the absolute spatial location of a previously conditioned flower and direct later choices to flowers marked by a echo-acoustic shape cue in common with the previously conditioned flower. Thus, the bats learnt both cues, but preferentially responded to the spatial over the shape cue when the two were placed in conflict.

A large amount of research has investigated animal use of geometry (the geometric shape of an experimental arena) and how this cue may be used in the presence/absence of featural cues (e.g. an object in the corner of an arena or a coloured wall, reviewed by Cheng and Newcombe 2005). Although the idea of a geometric module (a cognitive mechanism dedicated to processing geometric information) was popular in the past (Cheng 1986), evidence against this theory has emerged (Graham et al. 2006; Pearce et al. 2006). Indeed, some authors now consider geometric cues to be a type of featural cue, rather than a spatial cue (Cheng 2008). From this perspective, it is difficult to interpret the findings of the many geometry studies from the perspective of animal use of featural versus configural information. We will not try to resolve this issue here and so, without discounting the potential importance of those studies, we will not review them further.

From the research surveyed above there seems to be no consistent pattern between food-storing and non-storing species in terms of their reported preferences for either configural or featural cues in foraging tasks. More food-storing birds have been reported to prefer configural cues than featural cues, although this is not unanimous and amongst the food-storing rodents no clear pattern of preference emerges. Among nectarivorous species there is a more consistent pattern of preferential use of configural over featural cues (though colour cues can be used non-preferentially). Non-storing, non-nectarivorous species appear to use both types of cues, with different species expressing preferences for one or other of the cue types. In addition, there is evidence that classifying one cue as preferred over another does not adequately describe complex interactions between featural and configural cue use in some species.

Broad categorisations of ecology have historically been applied to predict/explain a range of psychological differences between species (such as food-storing versus non-storing, monogamy versus polygyny, social versus solitary), with varying degrees of success. We suggest, however, that such broad generalisations average over important aspects of species' ecology that would be expected to have influenced their psychological makeup. Indeed, the literature reviewed above suggests that any ultimate explanation of an animal's use of featural versus configural cues demands a more detailed consideration of the potential interactions between species ecology and task demands.

The purpose of the current paper is to further investigate the differential use of featural and configural cues in a variety of species with contrasting foraging ecologies. While the hypothesis that preferential attention to configural over featural cues is an adaptation to food-storing has endured for quite some time, the evidence for this hypothesis is not overwhelmingly convincing. We argue that a more detailed consideration of ecology and phylogeny is needed to properly understand animal use of concurrent, redundant and conflicting cues. To that end, we present data from three species: (i) omnivorous noisy miners that feed on both nectar and invertebrates; (ii) food-storing generalist Siberian jays; and (iii) kea parrots whose foraging can be described as opportunistic and innovative, often involving physical manipulation of the environment such as digging up buried larvae and plant roots, attacking live sheep and carcasses to access kidneys and other highly valued tissues (Huber and Gajdon 2006), and raiding human rubbish dumps (Jarrett and Wilson 1999).

## Noisy miners (*Manorina melanocephala*)

### Methods

#### *Subjects*

Fifteen noisy miners served as subjects in this study. The birds were trapped in the wild as adults (exact age and sex unknown) and held in individual cages measuring 3m x 3m x 3m for the duration of their time in captivity. Prior to the study reported here, the birds had not completed any other experimental study in spatial or colour learning, but some of the birds had participated in social learning studies in which they were taught how to peck through a paper covering to obtain mealworms in a dish below. The birds were maintained on a diet of Wombaroo Lorikeet and Honeyeater Wet Mix (a commercial nectar replacement) and once testing with the birds was complete, they were banded and released back into the territories from which they were caught.

### *Materials*

The experimental feeders consisted of small plastic wells (approx 1ml capacity) with lids, which the birds were pre-trained to open. These feeders were attached to the front of the cage in such a way that the small well fitted through a hole in the cage so that the birds inside could easily access it. Small painted timber squares (10cm x 10cm) were placed behind each feeder to act as colour cues. The feeders themselves were all grey, and the painted colour squares (in white, black, yellow, red, green, blue, orange and purple) indicated the colours to be returned to or avoided. Whether visiting a particular feeder was rewarded or not varied from trial to trial such that birds were only required to respond to colour information within a trial (Experiment 1), or rewards were consistent from trial to trial such that birds had to learn longer-term associations between a particular colour and the reward (Experiment 2). Feeders were baited with half a mealworm (*Tenebrio molitor* larvae).

### *Pre-training*

For all birds the pre-training consisted of placing a few baited feeders with the lids propped open (without the colour square attached) on the front wall of their cages. Once birds were readily approaching the feeders and consuming the rewards, the feeders were presented with the lids closed. It typically took the birds no more than a few attempts at a closed feeder to successfully open the lid. Pre-training ended when a bird was readily approaching closed feeders, opening them and retrieving baits.

### *Experiment 1*

Initially, eight subjects were used in a colour win-stay procedure, where the birds were reinforced for correctly matching the colour of experimental feeders. Thirty trials were initially conducted. Each trial consisted of an exploration phase and a test phase. In the exploration phase birds were presented with two feeders of different colours (randomly chosen), on the front wall of their cage. One of these feeders was baited. For four of the birds the feeders were placed approximately 2m apart, for the other four birds the feeders were placed immediately side-by-side in the middle of the cage front. Each bird was allowed to explore these feeders and consume the bait. Rather than chase birds way from the array, we allowed them to leave of their own volition after exploring the feeders. The majority of the time birds left the array after probing each feeder once, but occasionally birds would probe one of the feeders a second time before leaving. As there was always only one bait available in this phase, there was the potential for birds to learn this and leave the array if they found the bait in the first feeder they visited without probing the second feeder. This also happened, but only rarely.

Following the exploration phase, a retention interval of 2min ensued. The birds were again presented with the same two feeders for the test phase and in this phase birds were permitted to visit one feeder only. The bait was always contained in the same coloured feeder as in the exploration phase. For all birds the feeders in the test phase were placed 2m apart. This meant that for half the birds the same two locations were used in exploration and test phases (with the same coloured feeders in the same places for half the trials and in opposite places for the other half). For the other half of the birds the feeders were in different locations in the exploration and test phases (for half the trials the same coloured feeders were in the left and right positions in both phases and for the other half of trials the feeders in the left and right positions were swapped between the exploration and test phase). Each bird completed up to three trials per day with a minimum inter-trial interval of 30min.

As there was no evidence that any of these eight birds were using colour cues to guide their choices, some additional trials were carried out. Firstly, an additional four birds were run through the same protocol as above, but with the exception that these birds were reinforced to win-shift away from the previously rewarded colour in the test phase. This was to determine that it was not just the nature of the win-stay task that was resulting in chance performance.

Secondly, four of the eight birds that participated in the colour win-stay and two of the four birds that participated in the colour win-shift task were given an extra approximately 20 trials (for exact numbers see Results section) to see whether their performance might improve with further reinforcement.

### *Experiment 2*

As there was no evidence that birds were responding to colour information in Experiment 1, we ran an additional three birds through a protocol that required them to learn, across trials, which colours were rewarded and which were not. This experiment was designed to determine whether the birds would respond to colour cues if there were no conflicting spatial cues (either configural or location cues). We were primarily interested in making sure that the birds were able to perceive the different colours and use them to guide their behaviour in some way. To try and make this as likely as possible we made several changes to the colour win-stay procedure adopted in Experiment 1.

In case interference between trials was one of the factors contributing to the poor performance in Experiment 1, where the rewarded colour varied from trial to trial, we decided to consistently reward the same three colours throughout this experiment (and not reward another three colours). The three rewarded colours were yellow, blue and red, while the three unrewarded colours were orange, green and purple (black and white were not used in this experiment). We also used two feeders of the rewarded and unrewarded colours, respectively, in each phase of the trials, to increase the amount of reinforcement the birds received, relative to Experiment 1. To prevent the use of location information, these feeders were presented in four randomly chosen locations out of a potential sixteen (see Fig.1) in the exploration phase and in a different four locations in the test phase. As in Experiment 1, birds were allowed to freely explore all feeders in the exploration phase. After the 2min retention interval birds were permitted to only visit two of the four feeders in the test phase.

This design meant that in any given test phase of a trial the birds could potentially use reliable colour information that was available to them from previous trials, and from the exploration phase of the current trial. Once birds had made one choice in the test phase, they could also use the outcome of that choice to guide their second choice (if rewarded go to the other feeder of the same colour, if unrewarded go to a feeder of a different colour). Although these multiple sources of information made it difficult to determine what information the birds were actually responding to, we felt the design maximised the

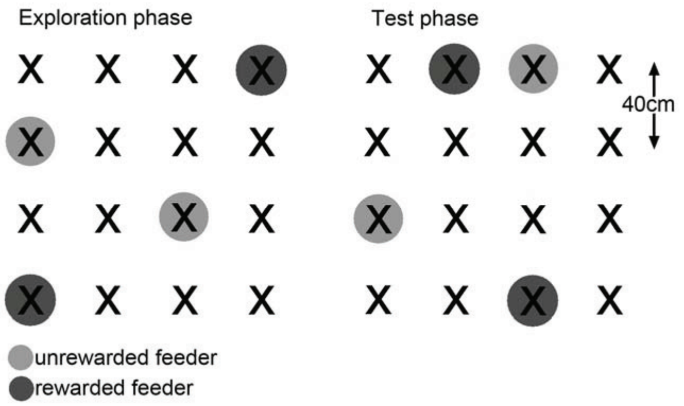

**Fig. 1** The locations of feeders used to test colour matching in the noisy miners, experiment 2. In the exploration phase of each trial two feeders of a rewarded colour and two feeders of an unrewarded colour were presented on the front wall of the birds' cage in four locations randomly chosen from a grid of sixteen possible locations. In the test phase the feeders were again presented in four randomly chosen locations with the only restriction being that none of the locations used in the exploration phase could also then be used in the test phase of any given trial.

likelihood that we would be able to confirm that the birds were capable of perceiving the colours and responding to them as a source of information. The three birds completed 24, 48 and 60 trials respectively, the variation being due to the amount of time the birds were available for testing. Birds completed six trials per day, with a minimum inter-trial interval of 30min.

## Results

### *Experiment 1*

If a bird found the correct feeder in the test phase they were given a score of one for that trial, otherwise they were given a score of zero. The initial thirty trials we conducted were broken up into six blocks (of 5 trials each) and a mean score for each block was calculated for each bird. These means were then analysed using a GLM repeated measures ANOVA with block (six levels, 1-6) as a within-subjects factor and feeder position in the exploration phase (2 levels, adjacent and apart) as a between subjects factor. Figure 2a shows that there was no evidence that the birds' performance improved over the course of the thirty trials, nor was it ever substantially above chance. This impression was confirmed by the analysis with neither the main effect of block ($F_{5,30} = 2.213$, $p = 0.079$) nor the block linear contrast ($F_{1,6} = 0.553$, $p = 0.485$) reaching significance. There were also no significant main effects or interactions involving the position (adjacent or apart) of the feeders in the exploration phase (all Fs < 0.5, all ps > 0.7). To confirm that the birds were not responding to the colour cues in this task, a series of one-sample t-tests were used to compare the birds' performance versus the chance value of 0.5, and this revealed that in none of the six blocks was the birds performance significantly above chance (all $t_7$s < 2, all ps > 0.1, uncorrected alpha values of 0.05 applied).

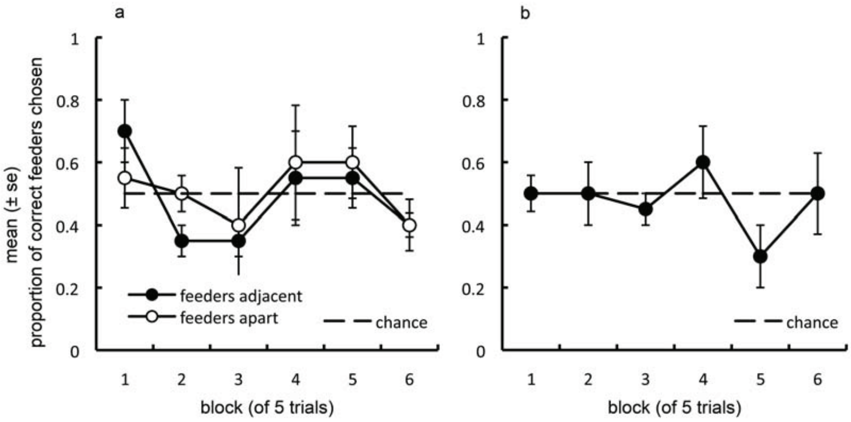

**Fig. 2** The mean (±) se proportion of correct feeders chosen in the five trials of each block of the noisy miners on the a) colour win-stay and b) colour win-shift versions of the task in experiment 1. In neither of these tasks were the birds able to perform significantly above chance.

The data from the additional four birds that completed a colour win-shift version of the task was analysed using a GLM ANOVA with block (six levels, 1-6) as a within-subjects factor. Due to a lack of power we did not factor the position of the feeder into the analysis. As Figure 2b shows there was also no evidence of learning in these trials (main effect of block, $F_{5,15} = 0.936$, $p = 0.486$; block linear contrast, $F_{1,3} = 0.201$, $p = 0.685$) and performance was never significantly nor substantially above chance (one-sample t-tests versus 0.5, all $t_3$s < 1, all ps > 0.4).

The last twenty extra trials completed by six of the birds were also broken up into four blocks (of 5 trials each) and were analysed with a GLM ANOVA with block (4 levels, 1-4) as the within-subjects factor. Once again there was no evidence of learning with neither the main effect of block ($F_{3,12} = 1.170$, $p = 0.362$) nor the block linear contrast ($F_{1,4} = 0.570$, $p = 0.492$) reaching significance. The six birds chose the correct feeder in 9, 9, 9, 10, 12 and 12 out of 20 trials, respectively, performance that was not significantly different from chance (binomial tests, all ps > 0.5, uncorrected alpha values applied).

An analysis of the locations, rather than the colours, that the birds chose to visit in the test phases of the trials, however, reveals a different story. Binomial tests analysing all of the trials each bird completed revealed that of the twelve birds tested, six displayed a significant bias to choose the feeder on either the left or the right side more than half the time. Runs tests showed that four of the six birds that did not display an overall side bias had a tendency to make repeated visits to the same side in consecutive trials followed by repeated visits to the other side. This left only two of the twelve birds displaying neither of these biases to a statistically significant extent. The results are displayed in Table 1.

**Table 1**. Noisy miner choices in experiment 1, showing the p-values associated with binomial and runs tests, examining the extent to which each individual bird displayed a bias to choose either the left or right feeder overall (binomial test), or in consecutive runs of trials (runs-test). Two-tailed asymptotic significances are shown, with significant results in bold.

| Bird | Reinforcement Contingency | Feeder Position | Trials Completed | No. Left | No. Right | Binomial P | Runs P |
|---|---|---|---|---|---|---|---|
| 4a | colour win-stay | adjacent | 30 | 26 | 4 | **<0.001** | |
| 2a | | | 30 | 20 | 10 | 0.099 | 0.944 |
| 3 | | | 55 | 22 | 33 | 0.177 | **0.001** |
| 1 | | | 50 | 25 | 25 | 1.000 | **0.045** |
| 1a | | apart | 30 | 23 | 7 | **0.005** | |
| 3a | | | 30 | 3 | 27 | **<0.001** | |
| 2 | | | 54 | 37 | 17 | **0.009** | |
| 4 | colour win-shift | adjacent | 53 | 24 | 29 | 0.583 | **<0.001** |
| 6a | | | 30 | 20 | 10 | 0.099 | 0.726 |
| 5 | | | 47 | 8 | 39 | **<0.001** | |
| 5a | | apart | 30 | 15 | 15 | 1.000 | **0.041** |
| 6 | | | 54 | 36 | 18 | **0.020** | |

*Experiment 2*

As can be seen in Figure 3, when just the first choice each bird makes in the test phase is analysed all three birds performed at chance levels seen in Experiment 1. They then increased their performance, however, to above chance levels as the trials progressed. Binomial tests revealed that two of the three birds chose a correct feeder in the test phase in significantly more than half the trials (bird 4b, p < 0.001; bird 8b, p = 0.046, one-tailed cumulative probability that birds would perform equal to or better than observed performance). Bird 2b actually performed better than the other two birds in blocks 3 and 4, but was only able to complete 24 trials, so a binomial test was not significant for the data from this bird (p = 0.154, two-tailed asymptotic significance). Interestingly, when just the second choice is examined, all three birds performed at close to chance levels (14

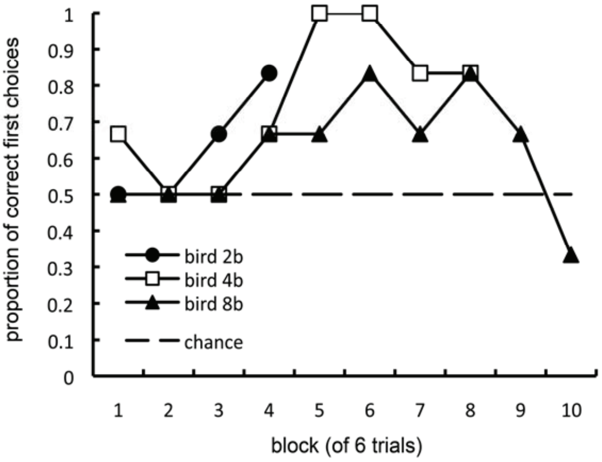

**Fig. 3** Proportion of first choices correct in the six trials of each block by each of the three noisy miner birds that participated in experiment 2. Two of three birds made correct choices significantly more often than expected by chance, demonstrating that the birds could perceive the different colours and could use this information to guide at least some of the foraging decisions.

out 24, 27 out of 48 and 27 out 60, respectively, all p-values > 0.2, one-tailed cumulative probability that birds would perform equal to or better then observed performance). This was likely due to the birds adopting a 'nearest neighbour' rule when searching the four feeders in the test phase. As the location of the four feeders was randomly chosen, the next nearest feeder to the first choice was equally likely to be correct as incorrect. Chance performance on the second choice of the test phase suggests that birds were not using feedback from their first choice to guide their second choice.

An examination of behaviour in the exploration phase suggests that at least one of the birds was using information gained from previous trials. When just the first feeder visited in each exploration phase is considered, bird 8A chose a rewarded feeder in 40 out of 60 trials (binomial test, p = 0.007, one-sided cumulative probability of equal or better performance than that observed, Bonferroni corrected alpha of 0.017 applied). The fact that the remaining two birds did not perform above chance on this measure (choosing rewarded feeders initially in 11 out of 24 and 25 out of 48 trials, respectively) is difficult to interpret as birds were permitted unlimited choices in this phase of a trial. Visits to unrewarded feeders were, therefore, not costly and so it is impossible to determine whether these two birds were sufficiently motivated to use long term colour information in the exploration phase. The above chance performance of bird 8b in the exploration phase and all birds in the test phase does, however, confirm that the birds were able to perceive the different colours and use this information over consecutive trials and days to guide their foraging behaviour.

## Siberian jays (*Perisoreus infaustus*)

### Methods

#### *Subjects*

This experiment was conducted in the field outside Arvidsjaur, northern Sweden, utilising a well-known study population of individually colour-banded and sexed wild Siberian jays (see Ekman et al. 2000, 2002). These territorial group-living birds are relatively tame and habituate easily to the presence of researchers at food sources. Seventeen birds (nine males, seven females and one of unknown sex), from six different social groups served as subjects.

#### *Materials*

The feeders consisted of three black plastic tubes, 150cm long and 6cm in diameter, that were positioned at approximately 45 degree angle from the experimenter down to the platform (of a top-pan balance) on the forest floor where the birds could stand. At the bird's end of the tube, we closed the end with black tape and cut off the top half of the tube creating a 6x6cm sized opening on the "front-side". When the experimenter inserted the food item at the top end of the tube it would roll down and be available for the birds within this opening. In the pre-training phase no colours were used, but in the experimental training and tests, the front side of the tubes were clearly labelled with coloured tape 18cm above the opening, and on the inside of the tube where the food items would land. When tubes were turned with the "front-side" down, the openings and colours were no longer visible for the birds, and we used this to indicate to the birds that the tube was closed and no reward could be obtained.

The food item rewards used were pieces of sausage, the weights of which depended upon the variance category of the tube. Mean reward was the same for all variance categories, but 'high variance' tubes were baited with either 0.5g or 2.5g of sausage (with equal probability), 'low variance' tubes with either 1.0g or 2.0g and 'no variance' tubes with 1.5g pieces on every occasion. A similar experiment with a different type of feeder confirmed that the Siberian jays in this population do have variance-sensitive foraging preferences and that they can use colours as cues for reward in this context (Ratikainen et al. 2010).

*Pre-training*

Pre-training began on 6th September 2006. As this study population was already well habituated to humans and readily took food items in the wild, all individuals initially had to be trained to stand still on one of three specific 5cm x 5cm spots on the 50cm x 30cm platform of the top-pan electronic balance. After five seconds, a reward piece of sausage was given by the experimenter through the plastic tube that corresponded to the one of the three spots on the platform chosen by the bird. When all individuals in the group seemed confident in performing this task, experimental training began.

*Experimental Procedure - Training*

Training sessions occurred from twice a day to once every second day and lasted between 30min and 1h to ensure that the extra food provided in these sessions remained an unpredictable resource. All subjects participated in at least fifteen training sessions before beginning the test sessions. Individual trials within the training sessions were designated as either free-choice or forced-choice.

Free-choice trials proceeded as follows. The three coloured tubes were placed in a row above the platform at a convenient location within the group territory. The position of each colour was randomly assigned for each training session and the high, low and no variance colours were also designated randomly for each social group (but held constant for each group throughout all the training and testing sessions). When a bird approached it was allowed to choose one of the tubes, by standing on the spot in front of the tube. The experimenter then delivered the appropriate reward through the tube. The bird had to leave the feeder before it was allowed to make another choice, and typically the birds would do so voluntarily because they would cache the food reward in nearby trees before they came back to the feeder.

To make sure that all individuals experienced all levels of variances, we carried out forced-choice trials interspersed with the free-choice trials. During forced-choice trials, only one tube was available for the birds to choose, the other two tubes were turned around, so that their openings were inaccessible, and they were showing a black surface only with no colour. In the beginning of the training period approximately every other visit to the feeder was a forced choice and the others were free choice. It was not possible, however, to keep to this schedule throughout, because of the order of the different visits of the different individual birds within each group. We did ensure, however, that forced-choices were divided equally between the three variances, and all three options were experienced many times over in random order by all individuals. To achieve this, towards the end of the training period, we carried out only forced-choice trials at the beginning of each session.

### *Experimental Procedure – Tests*

Test sessions were conducted between 10th and 15th of October, 2006. Each test session lasted 45min and consisted of free choice trials only. The choices made by each individual bird were recorded by the experimenter. Six test sessions were conducted within the territory of each of the six social groups. In each testing session the tubes were placed in one of the six possible arrangements (from left to right), in random order. Fifteen of the seventeen subjects were present for all six sessions, the remaining two subjects completing five and four testing sessions, respectively.

## Results

The total number of times a bird chose each of the three tubes was calculated for each testing session. Since the number of choices made within a testing session varied from bird to bird, we divided these tallies for each session by the total number of choices made by that bird in that session. We then calculated for each of the seventeen birds the mean proportion of choices allocated to each tube across all test sessions, categorising the tubes by both colour and location. In this way, each bird ended up with six means: the mean proportion of visits allocated to the red, green and yellow feeders and the mean proportion of visits allocated to the left, middle and right feeders. These mean proportions were then used to rank the three colours and three locations from least to most favoured for each individual bird. We then ran a series of partial correlations to determine the amounts of variance in individual choices that could be explained by preferences for particular colours and for particular locations respectively.

The data we correlated were number of choices made in each testing session against the colour of the feeders (ordered from least to most favoured), controlling for location (ordered from least to most favoured) and against the location of the feeders controlling for colour. The resulting r and p-values are presented in Table 2.

Partial correlations revealed that the location of the feeders explained a significant amount of the variance in feeder choice for thirteen of the seventeen birds, while feeder colour only explained a significant amount of the variance for six of the birds. It is important to note that the strength of all of the above correlations are potentially artificially increased since the preferences for feeders displayed by each individual bird were used to determine the ordinal rankings given to each colour and location, respectively. Therefore, rather than relying on the absolute significance or otherwise of the individual correlations, we z'-transformed all the r-values (for normality) and then applied a paired-samples t-test to the resulting lists of z-values. This test confirmed that configural location information explained a significantly higher proportion of the variance than colour information ($t_{16} = 3.469$, $p = 0.003$).

**Table 2.** The r and p-values associated with partial correlations between the number of visits that individual Siberian jays made to feeders and the colour of the feeders (controlling for feeder location) and between the number of visits and the configural location of the feeders (controlling for feeder colour). Two-tailed asymptotic significances are shown, with significant results in bold.

| Bird ID | Colour | | Location | |
|---|---|---|---|---|
| | r | p | r | p |
| 5 | 0.405 | 0.151 | **0.717** | **0.004** |
| 6 | 0.266 | 0.302 | **0.868** | **<0.001** |
| 10 | **0.604** | **0.010** | 0.355 | 0.162 |
| 11 | 0.247 | 0.338 | **0.863** | **<0.001** |
| 12 | 0.348 | 0.171 | 0.252 | 0.329 |
| 13 | -0.121 | 0.645 | **0.607** | **0.010** |
| 15 | 0.478 | 0.052 | **0.832** | **<0.001** |
| 16 | 0.202 | 0.437 | **0.562** | **0.019** |
| 17 | **0.519** | **0.033** | **0.772** | **<0.001** |
| 19 | **0.505** | **0.039** | **0.589** | **0.013** |
| 20 | 0.322 | 0.334 | 0.322 | 0.334 |
| 21 | **0.669** | **0.003** | **0.509** | **0.037** |
| 22 | **0.588** | **0.013** | 0.342 | 0.179 |
| 28 | 0.309 | 0.228 | **0.830** | **<0.001** |
| 29 | **0.531** | **0.028** | **0.793** | **<0.001** |
| 30 | 0.406 | 0.106 | **0.623** | **0.008** |
| 34 | -0.023 | 0.931 | **0.725** | **<0.001** |

## Kea (*Nestor notabilis*)

### Methods

#### *Subjects*

Ten kea (out of a captive group of 12, held at the Konrad-Lorenze Institut in Vienna, Austria) were used in the experiments. All subjects were males. Six were adults that had been raised in captivity by their parents, and four were hand-raised sub-adults, and so all birds were very familiar with humans. With the exception of one male, all kea were reared at the institute where they were permanently held in an outdoor aviary measuring 15m wide x 10m deep x 4m high, a space that could be separated into three 5m wide compartments. One of these compartments was used to run the experiment. During testing, opaque sliding doors separated the test compartment (and the bird in it) from the rest of the aviary.

#### *Materials*

Two types of feeder covers were used as the featural cues in this experiment: (i) smooth timber boards (measuring 12cm x 12cm x 2cm); and (ii) irregularly sized and shaped pieces of bark. Although the size of the pieces of bark was not uniform, they were not substantially smaller or larger than the timber boards. These covers were placed in the aviary (without any food underneath) for one day prior to the start of testing to allow the kea to habituate to their presence. The arrangement of the covers during testing is shown in Figure 4. For half the kea the bark was the cover containing food (as indicated in Figure 4) and for the remaining birds, the timber was the cover that contained food. For those birds for whom timber was the cover that contained food, the arrangement of covers shown in Figure 4 is reversed (bark replaced by timber and timber replaced by

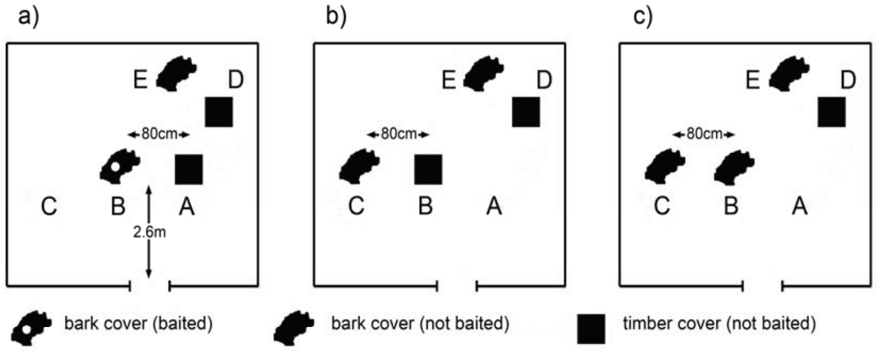

**Fig. 4** The placement of the bark and timber covers for kea during: (a) the pre-training and training trials of sessions 1 and 2; (b) the transfer tests of session 1 and 2; and (c) the control trial in session 2. The configuration shown was used when birds were trained with the reward under the bark cover. For those birds trained with the reward under the timber cover the locations of the bark and timber were reversed, relative to those shown above (with the exception of the covers at locations D and E – these were as shown for all birds).

bark) with the exception of the covers shown at locations E and D. These covers were held constant for all birds. The rewards used in these experiments were peanuts.

*General Procedure*

The study was conducted at the beginning of June 2007, over three consecutive days. Five subjects were randomly selected for testing on the first day, and the remaining five were tested on the second day. On the third day, six individuals were selected to continue in the experiment, as described below. From hereon in, we will refer to the trials run on the first and second day as session 1 and those run on the third day as session 2. All birds were tested individually in the test compartment and whenever one of the experimenters was manipulating the covers, a second experimenter held a board up to prevent the local enhancement from influencing the behaviour of the test bird.

*Session 1*

This session was divided into pre-training, training trials, a transfer test and a reminder training trial.

*Pre-training*

Each kea (individually) was given five minutes to freely explore the test compartment, with covers containing no food in place. During this five-minute period none of the kea spontaneously turned over any of the covers. Subsequently, the test bird was led out of the test compartment and three peanut seeds were placed at the cover at location B (see Figure 4a). One of these seeds was placed below the cover, the other two seed were protruding from underneath the cover. The bird was then allowed back into the test compartment for a further three minutes (at most) to find and consume the peanuts. Pre-training was considered complete if the bird retrieved all three peanut seeds. Seven of the ten subjects recovered both the visible and hidden peanut seeds on the first attempt. A further two subjects retrieved the visible seeds at the first attempt and all seeds at the second attempt. The last subject failed to retrieve any of the seeds over six attempts (conducted over two days) and so was not tested further.

*Training trial*

Immediately following pre-training, a single training trial was conducted in which one peanut seed was completely hidden under the cover at location B. All nine of the remaining birds successfully completed this trial on the first attempt, finding the seed within 16s maximum.

*Transfer test*

The transfer test consisted of a single trial in which the covers that had been at locations A and B were both shifted sideways to locations B and C, respectively (Figure 4b). This resulted in the previously rewarded cover now being 80cm further to the left, while the previously rewarded location now contained the other non-rewarded cover. This trial was designed to test whether the kea would prefer to choose the previously rewarded feature (the correct cover) or the previously rewarded location. None of the locations were baited during the transfer test.

*Reminder training trial*

Following the transfer test, a repeat of the training trial was given to each bird to reinstate the cover/location-food association.

*Session 2*

Six of the nine kea directed their initial searching toward the previously rewarded cover in session 1 rather than toward the previously rewarded location (see results), and these birds were selected to continue testing in session 2. Three of these birds had food associated with bark and three with timber in session 1 and these associations were retained for session 2. As in session 1, session 2 was divided into pre-training, training trials, transfer trials, and reminder training trials. All birds were then given an additional transfer test.

*Pre-training, and training, transfer and reminder trials*

Pre-training and training trials followed the same procedure as in session 1 except that pre-training was limited to 90s and five training trials were conducted, limited to 30s each. These were followed by a transfer test (where the two covers were shifted to the left) and then two reminder trials. The transfer tests and reminder trials followed the same procedure as in session 1.

*Control trial*

The final stage of the experiment was a control trial. This was conducted to test whether the kea's spatial memory for the location of the food was sufficiently precise to allow it to distinguish between the two locations presented in the transfer test and to determine whether the kea would tend to exhibit a novelty preference, choosing to inspect a cover at a site where no cover had previously been placed. In this trial, the rewarded cover was presented in the previously rewarded location, while a second cover of the same type was presented 80cm to the left (Figure 4c; the cover in location B was removed). Thus, the two covers closest to the birds as they entered the test compartment were both of the type previously associated with food. One cover was in the location most recently rewarded, while the other was 80cm to the left. Neither cover was baited and the trial lasted 30s.

## Results

### *Session 1*

On the first *training trial* (with no food directly visible), all nine kea first turned over the cover in location B. In the *transfer test*, in which covers A and B were shifted to the left (to B and C), five birds first turned over a cover at C (following the visual features), and one bird first turned over a cover at location E (at the back of the aviary), which was featurally the same as B had been in training. The shift from all nine birds choosing location B during training to only three birds choosing this location in the transfer test is significant (2-tailed Fisher's exact test: p=0.009).

### *Session 2*

In the last of the five additional *training trials* of session 2, all six birds searched first in location B, whereas only 1 bird searched first at location B in the *transfer test* (2-tailed Fisher's exact test: p=0.015) - again one bird first turned over the cover at the back of the aviary that matched the previously rewarded feature. In the *control trial* in session 2, however, when both shifted covers had the same features as the previously rewarded cover, all six kea first turned over the cover at the previously rewarded location B.

### *Turning over covers at the back*

The two covers at the back of the aviary, in locations D and E. were never shifted and were never rewarded by the experimenter. The results reported above refer only to the first cover that each bird turned over in each trial. Following their initial choice, however, the kea tended to continue to explore the aviary and turn over more covers. The kea turned over the cover at the back that featurally matched the rewarded cover at the front an average of six times (per bird) during the experiment. In contrast, the featurally non-matching cover was turned only once, on average (Wilcoxon signed-rank test, n=9, $\chi^2$ = -2.490, p = 0.013).

## General Discussion

In our experiments, both noisy miners and Siberian jays showed a significant preference to use spatial over colour information in tasks where only the colour information was reliable for predicting rewards, even though both species have shown an ability to use colour information when spatial information was rendered unavailable (noisy miners: experiment 2, Siberian jays: Ratikainen et al. 2010). The kea, on the other hand, showed a preference to visit feeder locations marked by a featural cue (cover type). This occurred when the featural cue was placed in direct conflict with a spatial location cue, and also manifested as the birds directed their search toward the rewarded feature compared to a similar unrewarded feature when both were at locations that had never been rewarded. Only when the featural cue didn't distinguish between the available options, did the kea base their choices on spatial location information.

All of the preferences shown should be seen in light of the ecology and foraging habits of the birds we tested. Both the noisy miner and the Siberian jay have evolved from ancestors that have foraging strategies that are hypothesised to favour use of spatial cues. Food-storing is likely the ancestral condition of the Corvid clade (de Kort and Clayton 2006), and the use of spatial cues shown by the Siberian jays in our study is consistent with the hypothesis that preferential attention to spatial cues is an adaptation to food-storing. While there is previous evidence that scatter hoarding birds are more likely to attend to spatial cues than their non-storing relatives, the majority of evidence for this comes from the Parid species (Brodbeck 1994, Brodbeck and Shettleworth 1995). The Siberian jay is the first food-storing corvid to demonstrate such a preference.

Previous studies demonstrating a preference for spatial cues in food-storing birds have tended to use a combination of cache-recovery paradigms, where birds are required to relocate food items they themselves cached, or associative paradigms, where birds must choose between previously rewarded and unrewarded locations/features. Species have tended to exhibit the same cue preference across both types of task (Shettleworth 1990; Shettleworth et al. 1990). The Siberian jays in the present study were required to retrieve food *de novo*, which they typically then cached before returning to retrieve more. The different choices provided rewards of different variances, rather than reward or no reward. In spite of these differences, the jays' preference for configural over featural cues is similar to that exhibited by food-storing Parids.

In a previous study with a similar task (Ratikainen et al. 2010) Siberian jays showed preference for the featural rather than the configural cue. The key difference between these studies may be the complexity of the configural cue. LaDage and colleagues (2009) demonstrated that food-storing chickadees (previously shown to prefer configural cues) prefer to use a featural cue when the configural cue consisted of the relative location of individual feeders in an array of 16 feeders, while the featural cue was that the target feeder was a different colour to the others. Ratikainen and colleagues (2010) presented birds with a board with 144 (12 x 12 rows) holes, of three different colours. Given the difficulty of recalling the spatial location of an individual hole based on the configuration of the holes, it is not surprising that the birds based their choice of hole on colour in that study. In the present study, however, the jays had a choice of only three tubes, whose relative locations could be much more easily discriminated.

The noisy miner evolved from a specialist nectarivore (Driskell and Christidis 2004), and their preference for spatial over featural cues is consistent with that observed in a wide variety of nectarivorous birds (Hurly and Healy 1996), bats (Carter et al. 2010) and insects (Ney-Nifle et al. 2001). Nectar is found in discrete, fixed locations, depletes after a single visit and replenishes reliably after a certain time period. This predictable spatio-temporal distribution may have selected for spatial cue-based foraging strategies. If a preference to attend to spatial cues is a general adaptive feature of nectarivorous species, then it is possible that noisy miners have inherited this tendency from a specialist nectarivore ancestor. However, the noisy miner is a generalist omnivore that feeds on invertebrates as well as nectar, and previous studies with the noisy miner have suggested that these birds respond with different cognitive strategies when searching for nectar versus invertebrates in the lab (Sulikowski and Burke 2007, Sulikowski and Burke 2010). Since birds in the current study were rewarded with invertebrates, we cautiously interpret the preference for spatial cues shown in the context of foraging for cryptic prey. No other studies have directly examined the differential use of spatial and featural cues in insectivorous species while foraging, but there is evidence that insectivorous birds use spatially-defined rules to search for cryptic prey (such as continuing along a straight path in the absence of prey, but turning in the same direction each time a prey item is encountered, to achieve area-restricted search, Smith 1974). Although plausible, further comparative data are needed before we could conclude with any certainty that foraging for cryptic prey may be associated with preferential use of spatial rather than featural cues when choosing locations to search. While much research has focused on the perceptual aspects of foraging for cryptic prey (e.g. Bond 2007, Ishii and Shimada 2010), we suggest that spatial information may guide decisions about where to search for such prey, while featural/visual cues may determine what is being searched for and whether a prey item is spotted.

The kea was the only species in our study to preferentially use featural over spatial cues to determine where to search. The kea used in the present study were reared in captivity, and so have no wild foraging experience. To the extent that cue preference may be dependent upon experience, caution must be exercised in the interpretation of the results obtained from the kea. The captive experience of the kea, however, with food consistently being provided in the same locations in the home aviaries, seems unlikely to have encouraged a feature-based search strategy in these birds.

The kea's preference for featural cues may reflect so-called structure-guided foraging (Menzel 1996), in which animals search in and around structures that are similar to other structures that have recently yielded food. Menzel (1996) suggested that such structure-guided foraging will be adaptive when species typically forage on the types of food that appear synchronously within the animals' environment (for example trees of the same species will fruit at the same time; mushrooms will sprout in damp shady areas after rain). Similar logic could be used to link the tendency of the kea to rely on featural cues to their reliance on roots as a food source (Clarke 1970). Although roots don't appear synchronously as in Menzel's theory, particular features of the aboveground plant could reliably indicate the presence of highly nutritious roots below. A preference to dig at plants that are featurally similar to other plants whose roots were nutritious could yield foraging benefits.

Given that the foraging ecology of the kea is characterised by innovation and opportunism (Huber and Gajdon 2006; Jarrett and Wilson 1999), however, we suggest an alternative explanation for the manifestation of structure guided foraging in this bird. Although the kea naturally exploits varied resources, attending to relevant structures to guide foraging may be a result of the innovativeness of the species, rather than a response to the distribution of any particular food resource. If a species forages in an opportunistic and innovative way, then the types of resources that it is likely to exploit will differ between individuals and generations. Under such a scenario, consistent selection pressure arising from the distribution of food resources (the selection pressure hypothesised to have resulted in greater attention to spatial cues in food-storing, nectarivorous and insectivorous species) would be lacking. On the other hand, an ability to generalise from a structure that has yielded a novel food resource to other visually similar structures could support innovative feeding behaviours. Consistent with this hypothesis, the few species that have been reported to preferentially attend to featural over spatial cues include the four species of great apes (Kanngeisser and Call 2010) whose innovation rates are high (Lefebvre et al. 2004) and the fox-squirrel (Waisman and Jacobs 2008) for whom innovation data are not published. Brown and Morgan (1995), however, report that fox-squirrels readily exploit novel food sources. Corvids are also cited as having high innovation rates (Lefebvre et al. 2004), but the data from Siberian jays in the present study indicate a preference for configural cues. This is not necessarily inconsistent with our innovation hypothesis, however, as many of the observations of innovative behaviour within the Corvids come from within the genus *Corvus*, the large-brained crows, which do not rely as heavily on caching as the jays used in the present research. We suggest that future studies comparing differential use of spatial and featural cues in species that differ in innovation rates may be profitable.

Implicit in many of the interpretations (including some of ours above) of the preferential use of either configural or featural cues is the notion that a species can be categorised as preferring one or other cue type, generally. We suggest that it may be more helpful, and is likely more realistic, for the default assumption to be that all animals have the potential to use featural and spatial information. It is the contexts in which each of these cues are used, and what they are used for, that is likely to vary within and between species for ecologically relevant reasons. For some species there may be very few contexts in which featural information is important, for other species featural information may be functionally relevant almost all the time. This perspective may not seem so different from suggesting that a particular species is either featurally biased or configurally biased generally, but it removes the need to categorise species using such black-and-white boundaries and allows for a more detailed understanding of why certain cues are favoured in certain circumstances. For example, food-storing bird species that have been shown to prefer configural cues will also use featural cues if the configural cue is sufficiently complex (LaDage et al. 2009, Ratikainen et al. 2010, and the present study). The point of relative cue complexity at which a given species shifts from one cue type to another may be a more informative correlate of species' ecology than which type of cue the species uses in any given task.

Differences in cue-preference between different experimental tasks could also reflect ecologically relevant contextual differences between the tasks. Featural cues may provide information about the ripeness of fruit (Willson and Whelan 1990), the toxicity of prey (Mallet and Joron 1999) and nectar and pollen yield from flowers (Gori 1989), and so may contribute to prey detection and decisions about whether to eat a particular item. Configural information, on the other hand, is important for knowing where specific patches are, their condition and estimating the travel between them (Charnov 1976), and for moving efficiently between multiple resource locations (Saleh and Chittka 2007). Therefore, all species may be more likely to use configural cues in a task requiring them to exploit a food resource in a fixed spatial location, but use featural cues at smaller scales to choose between available alternative food types. The distinction between these two categories of foraging decision has been present within optimal foraging theory for decades in the form of 'patch' versus 'diet' models (see Stephens et al. 2007). Patch models investigate 'exploitation' decisions, such as optimal leaving rules in the presence of patch depletion. Diet models examine 'attack' choices of which prey to feed upon once within a patch. One obvious challenge is in knowing which class of patch/configural versus diet/featural problem the animal is facing, or thinks it is facing, in any given foraging context. This is because we need to know the spatial scale at which patches are differentiated by the animal. When a single food location within a feeder array constitutes a 'patch', there is no 'diet' choice and we expect only configural cues to be used. However, in an apparently identical situation, where the whole feeder could constitutes a 'patch' and each food item is therefore a 'diet choice', we expect only featural cues to be used. Equally, when configural cues are used we might expect diet models to provide a better understanding of the choices made, and when featural cues are used then patch models should provide greater explanatory power of any foraging behaviour. We therefore suggest that a combination of comparative cognition and behavioural ecology approaches could provide opportunities to triangulate between cue use, perceptual context and optimal foraging choices, providing a potential novel solution to this problem.

## Conclusions

We present results from three different foraging tasks carried out on three very different bird species, which confirm the pattern we report in the literature, that there are no easy taxonomic generalizations when it comes to the use of featural versus configural cues. The specific cues that individual animals prefer to use in any experimental paradigm are likely to differ between species and situations (e.g. ecology, individual experience, etc.). We can, however, offer some potentially useful hypotheses that warrant further investigation: i) that a preferential attention for configural cues may be the norm across a wide variety of species when making decisions about *where* to search for food, such as the return to specific food sources; ii) that preferential use of featural cues may guide decisions about *whether* to exploit a food source, once the possible location of one (or more) food sources is known; and iii) that preferential use of featural over configural cues when searching for food, whilst apparently rare, may be associated with a high foraging innovation rate. As we have argued above, the solutions that animals use in any instance will depend upon important details concerning species ecology, individual experience, and the specific features of the task demands involved. Therefore, it is important to emphasise that any complete explanation of cue preference will take into account not only the general ecology of the species in question, but also which aspect of that ecology any given task represents.

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## Ethical Standards

The experiments described herein comply with the current laws of the countries in which they were performed.

## Conflict of Interest

The authors declare that they have no conflict of interest.

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# paper IV

Paper IV is not included in the electronic version

# paper V

Paper V is not included in the electronic version

# Doctoral theses in Biology
# Norwegian University of Science and Technology
# Department of Biology

| Year | Name | Degree | Title |
|---|---|---|---|
| 1974 | Tor-Henning Iversen | Dr. philos<br>Botany | The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism |
| 1978 | Tore Slagsvold | Dr. philos<br>Zoology | Breeding events of birds in relation to spring temperature and environmental phenology |
| 1978 | Egil Sakshaug | Dr.philos<br>Botany | "The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton" |
| 1980 | Arnfinn Langeland | Dr. philos<br>Zoology | Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake |
| 1980 | Helge Reinertsen | Dr. philos<br>Botany | The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton |
| 1982 | Gunn Mari Olsen | Dr. scient<br>Botany | Gravitropism in roots of *Pisum sativum* and *Arabidopsis thaliana* |
| 1982 | Dag Dolmen | Dr. philos<br>Zoology | Life aspects of two sympartic species of newts (*Triturus, Amphibia*) in Norway, with special emphasis on their ecological niche segregation |
| 1984 | Eivin Røskaft | Dr. philos<br>Zoology | Sociobiological studies of the rook *Corvus frugilegus* |
| 1984 | Anne Margrethe Cameron | Dr. scient<br>Botany | Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinzing hormone in male mature rats |
| 1984 | Asbjørn Magne Nilsen | Dr. scient<br>Botany | Alveolar macrophages from expectorates – Biological monitoring of workers exosed to occupational air pollution. An evaluation of the AM-test |
| 1985 | Jarle Mork | Dr. philos<br>Zoology | Biochemical genetic studies in fish |
| 1985 | John Solem | Dr. philos<br>Zoology | Taxonomy, distribution and ecology of caddisflies (*Trichoptera*) in the Dovrefjell mountains |
| 1985 | Randi E. Reinertsen | Dr. philos<br>Zoology | Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds |
| 1986 | Bernt-Erik Sæther | Dr. philos<br>Zoology | Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach |
| 1986 | Torleif Holthe | Dr. philos<br>Zoology | Evolution, systematics, nomenclature, and zoogeography in the polychaete orders *Oweniimorpha* and *Terebellomorpha*, with special reference to the Arctic and Scandinavian fauna |
| 1987 | Helene Lampe | Dr. scient<br>Zoology | The function of bird song in mate attraction and territorial defence, and the importance of song repertoires |
| 1987 | Olav Hogstad | Dr. philos<br>Zoology | Winter survival strategies of the Willow tit *Parus montanus* |
| 1987 | Jarle Inge Holten | Dr. philos<br>Botany | Autecological investigations along a coust-inland transect at Nord-Møre, Central Norway |

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|---|---|---|---|
| 1987 | Rita Kumar | Dr. scient<br>Botany | Somaclonal variation in plants regenerated from cell cultures of *Nicotiana sanderae* and *Chrysanthemum morifolium* |
| 1987 | Bjørn Åge Tømmerås | Dr. scient.<br>Zoolog | Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction |
| 1988 | Hans Christian Pedersen | Dr. philos<br>Zoology | Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care |
| 1988 | Tor G. Heggberget | Dr. philos<br>Zoology | Reproduction in Atlantic Salmon (*Salmo salar*): Aspects of spawning, incubation, early life history and population structure |
| 1988 | Marianne V. Nielsen | Dr. scient<br>Zoology | The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (*Mytilus edulis*) |
| 1988 | Ole Kristian Berg | Dr. scient<br>Zoology | The formation of landlocked Atlantic salmon (*Salmo salar* L.) |
| 1989 | John W. Jensen | Dr. philos<br>Zoology | Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth |
| 1989 | Helga J. Vivås | Dr. scient<br>Zoology | Theoretical models of activity pattern and optimal foraging: Predictions for the Moose *Alces alces* |
| 1989 | Reidar Andersen | Dr. scient<br>Zoology | Interactions between a generalist herbivore, the moose *Alces alces*, and its winter food resources: a study of behavioural variation |
| 1989 | Kurt Ingar Draget | Dr. scient<br>Botany | Alginate gel media for plant tissue culture |
| 1990 | Bengt Finstad | Dr. scient<br>Zoology | Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season |
| 1990 | Hege Johannesen | Dr. scient<br>Zoology | Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung |
| 1990 | Åse Krøkje | Dr. scient<br>Botany | The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test |
| 1990 | Arne Johan Jensen | Dr. philos<br>Zoology | Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmion (*Salmo salar*) and brown trout (*Salmo trutta*): A summary of studies in Norwegian streams |
| 1990 | Tor Jørgen Almaas | Dr. scient<br>Zoology | Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues |
| 1990 | Magne Husby | Dr. scient<br>Zoology | Breeding strategies in birds: Experiments with the Magpie *Pica pica* |
| 1991 | Tor Kvam | Dr. scient<br>Zoology | Population biology of the European lynx (*Lynx lynx*) in Norway |
| 1991 | Jan Henning L'Abêe Lund | Dr. philos<br>Zoology | Reproductive biology in freshwater fish, brown trout *Salmo trutta* and roach *Rutilus rutilus* in particular |
| 1991 | Asbjørn Moen | Dr. philos<br>Botany | The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands |
| 1991 | Else Marie Løbersli | Dr. scient<br>Botany | Soil acidification and metal uptake in plants |
| 1991 | Trond Nordtug | Dr. scient<br>Zoology | Reflctometric studies of photomechanical adaptation in superposition eyes of arthropods |
| 1991 | Thyra Solem | Dr. scient<br>Botany | Age, origin and development of blanket mires in Central Norway |

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|---|---|---|---|
| 1991 | Odd Terje Sandlund | Dr. philos Zoology | The dynamics of habitat use in the salmonid genera *Coregonus* and *Salvelinus*: Ontogenic niche shifts and polymorphism |
| 1991 | Nina Jonsson | Dr. philos | Aspects of migration and spawning in salmonids |
| 1991 | Atle Bones | Dr. scient Botany | Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase) |
| 1992 | Torgrim Breiehagen | Dr. scient Zoology | Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher |
| 1992 | Anne Kjersti Bakken | Dr. scient Botany | The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (*Phleum pratense* L.) |
| 1992 | Tycho Anker-Nilssen | Dr. scient Zoology | Food supply as a determinant of reproduction and population development in Norwegian Puffins *Fratercula arctica* |
| 1992 | Bjørn Munro Jenssen | Dr. philos Zoology | Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks |
| 1992 | Arne Vollan Aarset | Dr. philos Zoology | The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans. |
| 1993 | Geir Slupphaug | Dr. scient Botany | Regulation and expression of uracil-DNA glycosylase and $O^6$-methylguanine-DNA methyltransferase in mammalian cells |
| 1993 | Tor Fredrik Næsje | Dr. scient Zoology | Habitat shifts in coregonids. |
| 1993 | Yngvar Asbjørn Olsen | Dr. scient Zoology | Cortisol dynamics in Atlantic salmon, *Salmo salar* L.: Basal and stressor-induced variations in plasma levels ans some secondary effects. |
| 1993 | Bård Pedersen | Dr. scient Botany | Theoretical studies of life history evolution in modular and clonal organisms |
| 1993 | Ole Petter Thangstad | Dr. scient Botany | Molecular studies of myrosinase in Brassicaceae |
| 1993 | Thrine L. M. Heggberget | Dr. scient Zoology | Reproductive strategy and feeding ecology of the Eurasian otter *Lutra lutra*. |
| 1993 | Kjetil Bevanger | Dr. scient. Zoology | Avian interactions with utility structures, a biological approach. |
| 1993 | Kåre Haugan | Dr. scient Bothany | Mutations in the replication control gene trfA of the broad host-range plasmid RK2 |
| 1994 | Peder Fiske | Dr. scient. Zoology | Sexual selection in the lekking great snipe (*Gallinago media*): Male mating success and female behaviour at the lek |
| 1994 | Kjell Inge Reitan | Dr. scient Botany | Nutritional effects of algae in first-feeding of marine fish larvae |
| 1994 | Nils Røv | Dr. scient Zoology | Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant *Phalacrocorax carbo carbo* |
| 1994 | Annette-Susanne Hoepfner | Dr. scient Botany | Tissue culture techniques in propagation and breeding of Red Raspberry (*Rubus idaeus* L.) |
| 1994 | Inga Elise Bruteig | Dr. scient Bothany | Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers |
| 1994 | Geir Johnsen | Dr. scient Botany | Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses |
| 1994 | Morten Bakken | Dr. scient Zoology | Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, *Vulpes vulpes* |

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| 1994 | Arne Moksnes | Dr. philos<br>Zoology | Host adaptations towards brood parasitism by the Cockoo |
| 1994 | Solveig Bakken | Dr. scient<br>Bothany | Growth and nitrogen status in the moss *Dicranum majus* Sm. as influenced by nitrogen supply |
| 1994 | Torbjørn Forseth | Dr. scient<br>Zoology | Bioenergetics in ecological and life history studies of fishes. |
| 1995 | Olav Vadstein | Dr. philos<br>Botany | The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions |
| 1995 | Hanne Christensen | Dr. scient<br>Zoology | Determinants of Otter *Lutra lutra* distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink *Mustela vision* |
| 1995 | Svein Håkon Lorentsen | Dr. scient<br>Zoology | Reproductive effort in the Antarctic Petrel *Thalassoica antarctica*; the effect of parental body size and condition |
| 1995 | Chris Jørgen Jensen | Dr. scient<br>Zoology | The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity |
| 1995 | Martha Kold Bakkevig | Dr. scient<br>Zoology | The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport |
| 1995 | Vidar Moen | Dr. scient<br>Zoology | Distribution patterns and adaptations to light in newly introduced populations of *Mysis relicta* and constraints on Cladoceran and Char populations |
| 1995 | Hans Haavardsholm Blom | Dr. philos<br>Bothany | A revision of the *Schistidium apocarpum* complex in Norway and Sweden |
| 1996 | Jorun Skjærmo | Dr. scient<br>Botany | Microbial ecology of early stages of cultivated marine fish; inpact fish-bacterial interactions on growth and survival of larvae |
| 1996 | Ola Ugedal | Dr. scient<br>Zoology | Radiocesium turnover in freshwater fishes |
| 1996 | Ingibjørg Einarsdottir | Dr. scient<br>Zoology | Production of Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*): A study of some physiological and immunological responses to rearing routines |
| 1996 | Christina M. S. Pereira | Dr. scient<br>Zoology | Glucose metabolism in salmonids: Dietary effects and hormonal regulation |
| 1996 | Jan Fredrik Børseth | Dr. scient<br>Zoology | The sodium energy gradients in muscle cells of *Mytilus edulis* and the effects of organic xenobiotics |
| 1996 | Gunnar Henriksen | Dr. scient<br>Zoology | Status of Grey seal *Halichoerus grypus* and Harbour seal *Phoca vitulina* in the Barents sea region |
| 1997 | Gunvor Øie | Dr. scient<br>Bothany | Eevalution of rotifer *Brachionus plicatilis* quality in early first feeding of turbot *Scophtalmus maximus* L. larvae |
| 1997 | Håkon Holien | Dr. scient<br>Botany | Studies of lichens in spurce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters |
| 1997 | Ole Reitan | Dr. scient.<br>Zoology | Responses of birds to habitat disturbance due to damming |
| 1997 | Jon Arne Grøttum | Dr. scient.<br>Zoology | Physiological effects of reduced water quality on fish in aquaculture |
| 1997 | Per Gustav Thingstad | Dr. scient.<br>Zoology | Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher |
| 1997 | Torgeir Nygård | Dr. scient<br>Zoology | Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as Biomonitors |

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| 1997 | Signe Nybø | Dr. scient. Zoology | Impacts of long-range transported air pollution on birds with particular reference to the dipper *Cinclus cinclus* in southern Norway |
| 1997 | Atle Wibe | Dr. scient. Zoology | Identification of conifer volatiles detected by receptor neurons in the pine weevil (*Hylobius abietis*), analysed by gas chromatography linked to electrophysiology and to mass spectrometry |
| 1997 | Rolv Lundheim | Dr. scient Zoology | Adaptive and incidental biological ice nucleators |
| 1997 | Arild Magne Landa | Dr. scient Zoology | Wolverines in Scandinavia: ecology, sheep depredation and conservation |
| 1997 | Kåre Magne Nielsen | Dr. scient Botany | An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in *Acinetobacter calcoacetius* |
| 1997 | Jarle Tufto | Dr. scient Zoology | Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models |
| 1997 | Trygve Hesthagen | Dr. philos Zoology | Population responces of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters |
| 1997 | Trygve Sigholt | Dr. philos Zoology | Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet |
| 1997 | Jan Østnes | Dr. scient Zoology | Cold sensation in adult and neonate birds |
| 1998 | Seethaledsumy Visvalingam | Dr. scient Botany | Influence of environmental factors on myrosinases and myrosinase-binding proteins |
| 1998 | Thor Harald Ringsby | Dr. scient Zoology | Variation in space and time: The biology of a House sparrow metapopulation |
| 1998 | Erling Johan Solberg | Dr. scient. Zoology | Variation in population dynamics and life history in a Norwegian moose (*Alces alces*) population: consequences of harvesting in a variable environment |
| 1998 | Sigurd Mjøen Saastad | Dr. scient Botany | Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity |
| 1998 | Bjarte Mortensen | Dr. scient Botany | Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro |
| 1998 | Gunnar Austrheim | Dr. scient Botany | Plant biodiversity and land use in subalpine grasslands. – A conservtaion biological approach |
| 1998 | Bente Gunnveig Berg | Dr. scient Zoology | Encoding of pheromone information in two related moth species |
| 1999 | Kristian Overskaug | Dr. scient Zoology | Behavioural and morphological characteristics in Northern Tawny Owls *Strix aluco*: An intra- and interspecific comparative approach |
| 1999 | Hans Kristen Stenøien | Dr. scient Bothany | Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts) |
| 1999 | Trond Arnesen | Dr. scient Botany | Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway |
| 1999 | Ingvar Stenberg | Dr. scient Zoology | Habitat selection, reproduction and survival in the White-backed Woodpecker *Dendrocopos leucotos* |
| 1999 | Stein Olle Johansen | Dr. scient Botany | A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis |

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| 1999 | Trina Falck Galloway | Dr. scient Zoology | Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.) |
| 1999 | Marianne Giæver | Dr. scient Zoology | Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gradus morhua*) in the North-East Atlantic |
| 1999 | Hans Martin Hanslin | Dr. scient Botany | The impact of environmental conditions of density dependent performance in the boreal forest bryophytes *Dicranum majus*, *Hylocomium splendens*, *Plagiochila asplenigides*, *Ptilium crista-castrensis* and *Rhytidiadelphus lokeus* |
| 1999 | Ingrid Bysveen Mjølnerød | Dr. scient Zoology | Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques |
| 1999 | Else Berit Skagen | Dr. scient Botany | The early regeneration process in protoplasts from *Brassica napus* hypocotyls cultivated under various g-forces |
| 1999 | Stein-Are Sæther | Dr. philos Zoology | Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe |
| 1999 | Katrine Wangen Rustad | Dr. scient Zoology | Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease |
| 1999 | Per Terje Smiseth | Dr. scient Zoology | Social evolution in monogamous families:<br>mate choice and conflicts over parental care in the Bluethroat (*Luscinia s. svecica*) |
| 1999 | Gunnbjørn Bremset | Dr. scient Zoology | Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions |
| 1999 | Frode Ødegaard | Dr. scient Zoology | Host spesificity as parameter in estimates of arhrophod species richness |
| 1999 | Sonja Andersen | Dr. scient Bothany | Expressional and functional analyses of human, secretory phospholipase A2 |
| 2000 | Ingrid Salvesen | Dr. scient Botany | Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture |
| 2000 | Ingar Jostein Øien | Dr. scient Zoology | The Cuckoo (*Cuculus canorus*) and its host: adaptions and counteradaptions in a coevolutionary arms race |
| 2000 | Pavlos Makridis | Dr. scient Botany | Methods for the microbial econtrol of live food used for the rearing of marine fish larvae |
| 2000 | Sigbjørn Stokke | Dr. scient Zoology | Sexual segregation in the African elephant (*Loxodonta africana*) |
| 2000 | Odd A. Gulseth | Dr. philos Zoology | Seawater tolerance, migratory behaviour and growth of Charr, (*Salvelinus alpinus*), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard |
| 2000 | Pål A. Olsvik | Dr. scient Zoology | Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway |
| 2000 | Sigurd Einum | Dr. scient Zoology | Maternal effects in fish: Implications for the evolution of breeding time and egg size |
| 2001 | Jan Ove Evjemo | Dr. scient Zoology | Production and nutritional adaptation of the brine shrimp *Artemia* sp. as live food organism for larvae of marine cold water fish species |
| 2001 | Olga Hilmo | Dr. scient Botany | Lichen response to environmental changes in the managed boreal forset systems |

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| 2001 | Ingebrigt Uglem | Dr. scient Zoology | Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.) |
| 2001 | Bård Gunnar Stokke | Dr. scient Zoology | Coevolutionary adaptations in avian brood parasites and their hosts |
| 2002 | Ronny Aanes | Dr. scient | Spatio-temporal dynamics in Svalbard reindeer (*Rangifer tarandus platyrhynchus*) |
| 2002 | Mariann Sandsund | Dr. scient Zoology | Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses |
| 2002 | Dag-Inge Øien | Dr. scient Botany | Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway |
| 2002 | Frank Rosell | Dr. scient Zoology | The function of scent marking in beaver (*Castor fiber*) |
| 2002 | Janne Østvang | Dr. scient Botany | The Role and Regulation of Phospholipase $A_2$ in Monocytes During Atherosclerosis Development |
| 2002 | Terje Thun | Dr.philos Biology | Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material |
| 2002 | Birgit Hafjeld Borgen | Dr. scient Biology | Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth |
| 2002 | Bård Øyvind Solberg | Dr. scient Biology | Effects of climatic change on the growth of dominating tree species along major environmental gradients |
| 2002 | Per Winge | Dr. scient Biology | The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in *Arabidopsis thaliana* and the Ral GTPase from *Drosophila melanogaster* |
| 2002 | Henrik Jensen | Dr. scient Biology | Causes and consequenses of individual variation in fitness-related traits in house sparrows |
| 2003 | Jens Rohloff | Dr. philos Biology | Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control |
| 2003 | Åsa Maria O. Espmark Wibe | Dr. scient Biology | Behavioural effects of environmental pollution in threespine stickleback *Gasterosteus aculeatur* L. |
| 2003 | Dagmar Hagen | Dr. scient Biology | Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach |
| 2003 | Bjørn Dahle | Dr. scient Biology | Reproductive strategies in Scandinavian brown bears |
| 2003 | Cyril Lebogang Taolo | Dr. scient Biology | Population ecology, seasonal movement and habitat use of the African buffalo (*Syncerus caffer*) in Chobe National Park, Botswana |
| 2003 | Marit Stranden | Dr.scient Biology | Olfactory receptor neurones specified for the same odorants in three related Heliothine species (*Helicoverpa armigera, Helicoverpa assulta* and *Heliothis virescens*) |
| 2003 | Kristian Hassel | Dr.scient Biology | Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum* |
| 2003 | David Alexander Rae | Dr.scient Biology | Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic environments |
| 2003 | Åsa A Borg | Dr.scient Biology | Sex roles and reproductive behaviour in gobies and guppies: a female perspective |
| 2003 | Eldar Åsgard Bendiksen | Dr.scient Biology | Environmental effects on lipid nutrition of farmed Atlantic salmon (*Salmo Salar* L.) parr and smolt |
| 2004 | Torkild Bakken | Dr.scient Biology | A revision of Nereidinae (Polychaeta, Nereididae) |
| 2004 | Ingar Pareliussen | Dr.scient Biology | Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar |

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| 2004 | Tore Brembu | Dr.scient Biology | Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in *Arabidopsis thaliana* |
| 2004 | Liv S. Nilsen | Dr.scient Biology | Coastal heath vegetation on central Norway; recent past, present state and future possibilities |
| 2004 | Hanne T. Skiri | Dr.scient Biology | Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (*Heliothis virescens, Helicoverpa armigera* and *Helicoverpa assulta*) |
| 2004 | Lene Østby | Dr.scient Biology | Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment |
| 2004 | Emmanuel J. Gerreta | Dr. philos Biology | The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania |
| 2004 | Linda Dalen | Dr.scient Biology | Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming |
| 2004 | Lisbeth Mehli | Dr.scient Biology | Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria* x *ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea* |
| 2004 | Børge Moe | Dr.scient Biology | Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage |
| 2005 | Matilde Skogen Chauton | Dr.scient Biology | Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples |
| 2005 | Sten Karlsson | Dr.scient Biology | Dynamics of Genetic Polymorphisms |
| 2005 | Terje Bongard | Dr.scient Biology | Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period |
| 2005 | Tonette Røstelien | ph.d Biology | Functional characterisation of olfactory receptor neurone types in heliothine moths |
| 2005 | Erlend Kristiansen | Dr.scient Biology | Studies on antifreeze proteins |
| 2005 | Eugen G. Sørmo | Dr.scient Biology | Organochlorine pollutants in grey seal (*Halichoerus grypus*) pups and their impact on plasma thyrid hormone and vitamin A concentrations |
| 2005 | Christian Westad | Dr.scient Biology | Motor control of the upper trapezius |
| 2005 | Lasse Mork Olsen | ph.d Biology | Interactions between marine osmo- and phagotrophs in different physicochemical environments |
| 2005 | Åslaug Viken | ph.d Biology | Implications of mate choice for the management of small populations |
| 2005 | Ariaya Hymete Sahle Dingle | ph.d Biology | Investigation of the biological activities and chemical constituents of selected *Echinops* spp. growing in Ethiopia |
| 2005 | Anders Gravbrøt Finstad | ph.d Biology | Salmonid fishes in a changing climate: The winter challenge |
| 2005 | Shimane Washington Makabu | ph.d Biology | Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana |
| 2005 | Kjartan Østbye | Dr.scient Biology | The European whitefish *Coregonus lavaretus* (L.) species complex: historical contingency and adaptive radiation |
| 2006 | Kari Mette Murvoll | ph.d Biology | Levels and effects of persistent organic pollutans (POPs) in seabirds<br>Retinoids and α-tocopherol – potential biomakers of POPs in birds? |

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| 2006 | Ivar Herfindal | Dr.scient Biology | Life history consequences of environmental variation along ecological gradients in northern ungulates |
| 2006 | Nils Egil Tokle | ph.d Biology | Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on *Calanus finmarchicus* |
| 2006 | Jan Ove Gjershaug | Dr.philos Biology | Taxonomy and conservation status of some booted eagles in south-east Asia |
| 2006 | Jon Kristian Skei | Dr.scient Biology | Conservation biology and acidification problems in the breeding habitat of amphibians in Norway |
| 2006 | Johanna Järnegren | ph.d Biology | Acesta Oophaga and Acesta Excavata – a study of hidden biodiversity |
| 2006 | Bjørn Henrik Hansen | ph.d Biology | Metal-mediated oxidative stress responses in brown trout (*Salmo trutta*) from mining contaminated rivers in Central Norway |
| 2006 | Vidar Grøtan | ph.d Biology | Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates |
| 2006 | Jafari R Kideghesho | ph.d Biology | Wildlife conservation and local land use conflicts in western Serengeti, Corridor Tanzania |
| 2006 | Anna Maria Billing | ph.d Biology | Reproductive decisions in the sex role reversed pipefish *Syngnathus typhle*: when and how to invest in reproduction |
| 2006 | Henrik Pärn | ph.d Biology | Female ornaments and reproductive biology in the bluethroat |
| 2006 | Anders J. Fjellheim | ph.d Biology | Selection and administration of probiotic bacteria to marine fish larvae |
| 2006 | P. Andreas Svensson | ph.d Biology | Female coloration, egg carotenoids and reproductive success: gobies as a model system |
| 2007 | Sindre A. Pedersen | ph.d Biology | Metal binding proteins and antifreeze proteins in the beetle *Tenebrio molitor*<br>- a study on possible competition for the semi-essential amino acid cysteine |
| 2007 | Kasper Hancke | ph.d Biology | Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae |
| 2007 | Tomas Holmern | ph.d Biology | Bushmeat hunting in the western Serengeti: Implications for community-based conservation |
| 2007 | Kari Jørgensen | ph.d Biology | Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth *Heliothis virescens* |
| 2007 | Stig Ulland | ph.d Biology | Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, (*Mamestra brassicae* L.) (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry |
| 2007 | Snorre Henriksen | ph.d Biology | Spatial and temporal variation in herbivore resources at northern latitudes |
| 2007 | Roelof Frans May | ph.d Biology | Spatial Ecology of Wolverines in Scandinavia |
| 2007 | Vedasto Gabriel Ndibalema | ph.d Biology | Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania |
| 2007 | Julius William Nyahongo | ph.d Biology | Depredation of Livestock by wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania |
| 2007 | Shombe Ntaraluka Hassan | ph.d Biology | Effects of fire on large herbivores and their forage resources in Serengeti, Tanzania |

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| 2007 | Per-Arvid Wold | ph.d Biology | Functional development and response to dietary treatment in larval Atlantic cod (*Gadus morhua* L.) Focus on formulated diets and early weaning |
| 2007 | Anne Skjetne Mortensen | ph.d Biology | Toxicogenomics of Aryl Hydrocarbon- and Estrogen Receptor Interactions in Fish: Mechanisms and Profiling of Gene Expression Patterns in Chemical Mixture Exposure Scenarios |
| 2008 | Brage Bremset Hansen | ph.d Biology | The Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and its food base: plant-herbivore interactions in a high-arctic ecosystem |
| 2008 | Jiska van Dijk | ph.d Biology | Wolverine foraging strategies in a multiple-use landscape |
| 2008 | Flora John Magige | ph.d Biology | The ecology and behaviour of the Masai Ostrich (Struthio camelus massaicus) in the Serengeti Ecosystem, Tanzania |
| 2008 | Bernt Rønning | ph.d Biology | Sources of inter- and intra-individual variation in basal metabolic rate in the zebra finch, (*Taeniopygia guttata*) |
| 2008 | Sølvi Wehn | ph.d Biology | Biodiversity dynamics in semi-natural mountain landscapes.<br>- A study of consequences of changed agricultural practices in Eastern Jotunheimen |
| 2008 | Trond Moxness Kortner | ph.d Biology | "The Role of Androgens on previtellogenic oocyte growth in Atlantic cod (*Gadus morhua*): Identification and patterns of differentially expressed genes in relation to Stereological Evaluations" |
| 2008 | Katarina Mariann Jørgensen | Dr.Scient Biology | The role of platelet activating factor in activation of growth arrested keratinocytes and re-epithelialisation |
| 2008 | Tommy Jørstad | ph.d Biology | Statistical Modelling of Gene Expression Data |
| 2008 | Anna Kusnierczyk | ph.d Bilogy | *Arabidopsis thaliana* Responses to Aphid Infestation |
| 2008 | Jussi Evertsen | ph.d Biology | Herbivore sacoglossans with photosynthetic chloroplasts |
| 2008 | John Eilif Hermansen | ph.d Biology | Mediating ecological interests between locals and globals by means of indicators. A study attributed to the asymmetry between stakeholders of tropical forest at Mt. Kilimanjaro, Tanzania |
| 2008 | Ragnhild Lyngved | ph.d Biology | Somatic embryogenesis in *Cyclamen persicum.* Biological investigations and educational aspects of cloning |
| 2008 | Line Elisabeth Sundt-Hansen | ph.d Biology | Cost of rapid growth in salmonid fishes |
| 2008 | Line Johansen | ph.d Biology | Exploring factors underlying fluctuations in white clover populations – clonal growth, population structure and spatial distribution |
| 2009 | Astrid Jullumstrø Feuerherm | ph.d Biology | Elucidation of molecular mechanisms for pro-inflammatory phospholipase A2 in chronic disease |
| 2009 | Pål Kvello | ph.d Biology | Neurons forming the network involved in gustatory coding and learning in the moth *Heliothis virescens:* Physiological and morphological characterisation, and integration into a standard brain atlas |
| 2009 | Trygve Devold Kjellsen | ph.d Biology | Extreme Frost Tolerance in Boreal Conifers |

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| 2009 | Johan Reinert Vikan | ph.d Biology | Coevolutionary interactions between common cuckoos *Cuculus canorus* and *Fringilla* finches |
| 2009 | Zsolt Volent | ph.d Biology | Remote sensing of marine environment: Applied surveillance with focus on optical properties of phytoplankton, coloured organic matter and suspended matter |
| 2009 | Lester Rocha | ph.d Biology | Functional responses of perennial grasses to simulated grazing and resource availability |
| 2009 | Dennis Ikanda | ph.d Biology | Dimensions of a Human-lion conflict: Ecology of human predation and persecution of African lions (*Panthera leo*) in Tanzania |
| 2010 | Huy Quang Nguyen | ph.d Biology | Egg characteristics and development of larval digestive function of cobia (*Rachycentron canadum*) in response to dietary treatments<br>-Focus on formulated diets |
| 2010 | Eli Kvingedal | ph.d Biology | Intraspecific competition in stream salmonids: the impact of environment and phenotype |
| 2010 | Sverre Lundemo | ph.d Biology | Molecular studies of genetic structuring and demography in *Arabidopsis* from Northern Europe |
| 2010 | Iddi Mihijai Mfunda | ph.d Biology | Wildlife Conservation and People's livelihoods: Lessons Learnt and Considerations for Improvements. Tha Case of Serengeti Ecosystem, Tanzania |
| 2010 | Anton Tinchov Antonov | ph.d Biology | Why do cuckoos lay strong-shelled eggs? Tests of the puncture resistance hypothesis |
| 2010 | Anders Lyngstad | ph.d Biology | Population Ecology of *Eriophorum latifolium*, a Clonal Species in Rich Fen Vegetation |
| 2010 | Hilde Færevik | ph.d Biology | Impact of protective clothing on thermal and cognitive responses |
| 2010 | Ingerid Brænne Arbo | ph.d Medical technology | Nutritional lifestyle changes – effects of dietary carbohydrate restriction in healthy obese and overweight humans |
| 2010 | Yngvild Vindenes | ph.d Biology | Stochastic modeling of finite populations with individual heterogeneity in vital parameters |
| 2010 | Hans-Richard Brattbakk | ph.d Medical technology | The effect of macronutrient composition, insulin stimulation, and genetic variation on leukocyte gene expression and possible health benefits |
| 2011 | Geir Hysing Bolstad | ph.d Biology | Evolution of Signals: Genetic Architecture, Natural Selection and Adaptive Accuracy |
| 2011 | Karen de Jong | ph.d Biology | Operational sex ratio and reproductive behaviour in the two-spotted goby (*Gobiusculus flavescens*) |
| 2011 | Ann-Iren Kittang | ph.d Biology | *Arabidopsis thaliana* L. adaptation mechanisms to microgravity through the EMCS MULTIGEN-2 experiment on the ISS:– The science of space experiment integration and adaptation to simulated microgravity |
| 2011 | Aline Magdalena Lee | ph.d Biology | Stochastic modeling of mating systems and their effect on population dynamics and genetics |
| 2011 | Christopher Gravningen Sørmo | ph.d Biology | Rho GTPases in Plants: Structural analysis of ROP GTPases; genetic and functional<br>studies of MIRO GTPases in *Arabidopsis thaliana* |
| 2011 | Grethe Robertsen | ph.d Biology | Relative performance of salmonid phenotypes across environments and competitive intensities |
| 2011 | Line-Kristin Larsen | ph.d Biology | Life-history trait dynamics in experimental populations of guppy (*Poecilia reticulata*): the role of breeding regime and captive environment |

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| 2011 | Maxim A. K. Teichert | ph.d Biology | Regulation in Atlantic salmon (*Salmo salar*): The interaction between habitat and density |
| 2011 | Torunn Beate Hancke | ph.d Biology | Use of Pulse Amplitude Modulated (PAM) Fluorescence and Bio-optics for Assessing Microalgal Photosynthesis and Physiology |
| 2011 | Sajeda Begum | ph.d Biology | Brood Parasitism in Asian Cuckoos: Different Aspects of Interactions between Cuckoos and their Hosts in Bangladesh |
| 2011 | Kari J. K. Attramadal | ph.d Biology | Water treatment as an approach to increase microbial control in the culture of cold water marine larvae |
| 2011 | Camilla Kalvatn Egset | ph.d Biology | The Evolvability of Static Allometry: A Case Study |
| 2011 | AHM Raihan Sarker | ph.d Biology | Conflict over the conservation of the Asian elephant (*Elephas maximus*) in Bangladesh |
| 2011 | Gro Dehli Villanger | ph.d Biology | Effects of complex organohalogen contaminant mixtures on thyroid hormone homeostasis in selected arctic marine mammals |
| 2011 | Kari Bjørneraas | ph.d Biology | Spatiotemporal variation in resource utilisation by a large herbivore, the moose |
| 2011 | John Odden | ph.d Biology | The ecology of a conflict: Eurasian lynx depredation on domestic sheep |
| 2011 | Simen Pedersen | ph.d Biology | Effects of native and introduced cervids on small mammals and birds |
| 2011 | Mohsen Falahati-Anbaran | ph.d Biology | Evolutionary consequences of seed banks and seed dispersal in *Arabidopsis* |
| 2012 | Jakob Hønborg Hansen | ph.d Biology | Shift work in the offshore vessel fleet: circadian rhythms and cognitive performance |
| 2012 | Elin Noreen | ph.d Biology | Consequences of diet quality and age on life-history traits in a small passerine bird |