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

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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 prewinter food-hoarding visits to experimental feeders. 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 are suggested to maximize both individual and group-wide foraging efficiencies when exploiting the ephemeral food sources typical of boreal taiga forests.

Information is valuable when it can tell animals something that allows them to change their behaviour in a way that will increase their payoffs (Gould 1974; Stephens 1989). To this end, sampling patches of uncertain quality provides information that improves foraging performance in a range of species (e.g. Krebs et al. 1978; Lima 1984, 1985; Valone 2006). Sampling can carry a short-term cost if the patch is poor, and the effort spent investigating the quality of unfamiliar patches must provide greater long-term benefits of more efficient foraging decisions from improved information. Such strategic problems are often solved using simplified 'rules of thumb' (McNamara & Houston 1980), which are behavioural approximations to the optimal solutions to problems. 'Win-stay lose-shift' is a simple rule of thumb for information use 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 & 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 & 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 & 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

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'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 estimate patch quality accurately (Valone & Templeton 2002). Public information is considered a benefit of group foraging (Clark & 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 & Giraldeau 1996; van Bergen et al. 2004).

In a system with foraging choices providing rewards 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 & Caraco 1986; McNamara & 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 living in boreal taiga forests close to Arvidsjaur in northern Sweden (65° 40′N, 19° 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 & Hogstad 2001). The jays 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 they have been 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, of 60 × 60 cm, and each board contained 12 plastic tubes sunken into the surface and organized in three patches (Fig. 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 12 patches of each of the three colours (see Fig. 1). All four tubes in a patch contained the same reward, that is, 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 consisted 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 randomized between groups, but kept constant throughout the experiment for a given group. The depletion of tubes within patches was easily recognized by the jays from a distance owing to the unambiguous position of the open lids and the jays were never observed attempting to find rewards in empty tubes. We therefore assume that the jays treated the empty tubes differently from the tubes left unopened and did not perceive the profitability or variance as changing as a result of depletion of patches throughout the sessions. No patches of the same colour were placed next to each other (see Fig. 1); and the relative spatial positions of patch type and profitability were randomized between sessions.

Our experiment contained two levels of information. First, 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