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Smit, Judith A.H.; van Oers, Kees

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Personality types vary in their personal and social information use

Judith A. H. Smit^{a, b}, Kees van Oers^{a, *}

^a Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, the Netherlands

^b Department of Ecological Science, Section Animal Ecology, Vrije Universiteit Amsterdam, Amsterdam, the Netherlands

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Gathering information about the environment, such as the location and quality of food, is crucial for an animal's survival, particularly in a changing environment. An animal can collect 'personal information' by interacting with the environment itself, or it can collect 'social information' by observing the behaviour of others. The use of these two types of information varies across different situations and between individuals. Personality is a concept that captures consistent interindividual differences in behaviour and could be one of the factors driving interindividual variation in information use. We tested this by conducting behavioural experiments based on a colour association task in captive great tits, *Parus major*, originating from lines bidirectionally selected for high and low exploratory behaviour. We quantified personal information use by measuring to what extent a bird relied on previously rewarded options instead of novel options. Social information use was measured by recording how birds chose according to social information provided by video playbacks of a conspecific. Here, we demonstrate that variation in the use of both personal and social information is indeed personality related. In their decision making, slow explorers relied more on prior knowledge, from both personal and social origins, whereas fast explorers tended to ignore the available information and chose more randomly. The differences between the personality types imply different costs or constraints in acquiring and/or applying the two types of information, possibly due to variation in, for example, cognitive styles. In conclusion, we demonstrate that personality types have different strategies to cope with environmental uncertainty.

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Using information from the environment, such as the location and quality of resources, is a crucial part of an animal's life, particularly in a changing environment. An animal constantly needs to make behavioural decisions and basing these decisions on information about various alternatives enhances an individual's fitness (McNamara & Dall, 2010). An individual can obtain information from two different sources, by interacting with the environment itself ('personal information') or by observing the behaviour of others ('social information') (Danchin, Giraldeau, Valone, & Wagner, 2004).

Personal information can be gathered when an individual adopts a trial-and-error tactic and observes cues from the physical environment (Danchin et al., 2004), also referred to as 'sampling behaviour'. In this way novel information can be generated, potentially leading to innovations. In contrast to personal information, the collection of social information is limited to situations

involving other individuals, usually conspecifics. To gather social information, cues or signals produced by others need to be accessible (Danchin et al., 2004). Nevertheless, the use of social information is ubiquitous throughout the animal kingdom and can occur in diverse contexts, such as foraging, mate choice or predator avoidance (Danchin et al., 2004).

The use of information, either socially or personally acquired, brings benefits in terms of more adaptive behavioural decisions (McNamara & Dall, 2010), but there are also costs associated with it (Kendal, Coolen, van Bergen, & Laland, 2005). Generally, the collection of social information is assumed to be less costly compared to personal information in terms of time, energy and predatory exposure (for a review see Kendal et al., 2005). Under some circumstances, however, for example when an animal cannot directly observe the cues on which a conspecific bases its behaviour, social information can be less reliable than personal information (Giraldeau, Valone, & Templeton, 2002). While in some situations it is possible to use both personal and social information simultaneously, the two types of information can conflict, or animals can be limited in sensing or processing both (Giraldeau et al., 2002). In such cases individuals need to decide whether to rely on

* Correspondence: K. van Oers, Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Droevendaalsesteeg 10, 6708 PB Wageningen, the Netherlands.

E-mail address: K.vanOers@nioo.knaw.nl (K. van Oers).

personally or socially acquired information or not to rely on previously obtained information at all.

The information use strategy that maximizes an animal's success varies between situations. For example, when the established behaviour proves unproductive or when the majority of conspecifics perform some behaviour, individuals should use social information (Laland, 2004). Furthermore, some characteristics, such as age, dominance or familiarity, can influence how likely it is that an individual is copied by observing conspecifics (Coussi-Korbel & Fragaszy, 1995; Laland, 2004). Consequently, optimality theory predicts that animals should be flexible and alter the value they attribute to personal and social information depending on circumstances (Laland, 2004; Rendell et al., 2011).

However, a growing body of evidence suggests that animals are limited in their flexibility to switch between information use strategies, indicating that there is individual variation in the preferred information source within a species (Boogert, Zimmer, & Spencer, 2013; Rosa, Nguyen, & Dubois, 2012). It has been shown in multiple species that some individuals consistently show a greater propensity to use social information than others (e.g. Dubois, Giraldeau, & Reale, 2012; Hämäläinen, Rowland, Mappes, & Thorogood, 2017; Rendell et al., 2011; Rosa et al., 2012). For example, in zebra finches, *Taeniopygia guttata*, the females that use most social information in a foraging context have been shown to use the most social information in a mating context as well (Rosa et al., 2012). Variation in information use might relate to an individual's physical characteristics, such as age (Thornton & Malapert, 2009), sex (Rendell et al., 2011; Rosa et al., 2012) or ontogeny (Boogert et al., 2013), as well as an animal's personality (e.g. Kurvers et al., 2010; Marchetti & Drent, 2000; Nomakuchi, Park, & Bell, 2009).

The phenomenon of 'animal personality' captures consistent interindividual differences in behaviour and has been described in numerous taxa (Reale, Reader, Sol, McDougall, & Dingemans, 2007). Personality encompasses several correlated traits often including boldness, activity and exploration, and the latter is generally used as an operational measure for personality (Reale et al., 2007). Animals are consistent in these personality traits across time and contexts (Reale et al., 2007), and this might impose constraints and affect the cost–benefit trade-offs associated with personal and social information use.

Relying on personal information instead of sampling the environment might be preferred by more exploratory and bolder individuals that are more routine prone. Fast-exploring great tits, *Parus major*, have been found to need more time to adjust to a changed location of food (Drent, Marchetti, 1999; Verbeek, Drent, & Wiepkema, 1994), indicating they might rely more on their personal knowledge. Slower exploring animals, on the other hand, are known to be more social (e.g. Van Oers, Klunder, & Drent, 2005), predicting that they rely more on social information. Shyer barnacle geese, *Branta leucopsis*, for example, have been shown to use more social information (Kurvers et al., 2010). Other studies in great tits and three-spined sticklebacks, *Gasterosteus aculeatus*, have also examined the relation between social information use and personality (Marchetti & Drent, 2000; Nomakuchi et al., 2009), but here it was impossible to separate social information use and sociability (the tendency to be close to conspecifics) because individuals needed to approach the demonstrator in order to collect information. Moreover, in the latter two studies individuals were able to collect personal and social information simultaneously, which made the measure of social information use less accurate.

The use of personal and social information cannot be seen as independent, however, since a trade-off between personal and social information might exist. Using more of one type of information might decrease the need to use the other. Additionally,

some individuals might base their behaviour more on information of any origin.

Individuals that are more behaviourally flexible, that is, are more able to respond to environmental stimuli, might use more information (Coppens, de Boer, & Koolhaas, 2010). Personality has been found to be related to behavioural flexibility (reviewed in Coppens et al., 2010; Mathot, Wright, Kempenaers, & Dingemans, 2012), and slow-exploring individuals seem to be the most flexible, implying that they use more information of any origin.

Surprisingly, until now only one study has examined both types of information use in relation to personality (Trompf & Brown, 2014). In this study female guppies, *Poecilia reticulata*, could decide between personal and social information when the two sources conflicted, and it was shown that boldness and sociality affected this decision (Trompf & Brown, 2014). What is currently lacking are studies that test individual differences in both personal and social information use in separate experiments, thereby taking the possibility that individuals might differ in the extent to which they rely on information of any source into account.

Therefore, the aim of this study was to shed light on how personality types vary in both personal and social information use. First, we predicted that faster exploring individuals would rely more on personal information, since they are known to be more routine prone (Drent & Marchetti, 1999; Verbeek et al., 1994). Second, we predicted that slower exploring individuals would use more social information because they are known to pay more attention to conspecifics (Harcourt, Ang, Sweetman, Johnstone, & Manica, 2009; Stöwe & Kotrschal, 2007; Van Oers et al., 2005). Lastly, since slower exploring individuals are known to be more behaviourally flexible (Coppens et al., 2010; Mathot et al., 2012), we predicted that they would also use more information overall.

To test our predictions, we used great tits originating from a bidirectional selection experiment on early exploratory behaviour, a validated measure of a personality trait in great tits. We performed two behavioural experiments based on a colour association task in which we quantified the tendency to use personal information, measured as choosing previously rewarded options, and the tendency to use social information provided by video playbacks.

METHODS

Study Subjects and Housing

Our test subjects were hand-reared captive great tits that were part of a bidirectional selection experiment on the personality trait 'exploratory behaviour' (Drent, van Oers, & van Noordwijk, 2003). As a measure of this personality trait the birds were tested for their 'early exploratory behaviour' (range 0–20), which was quantified by a combination of a novel environment test and two novel object tests (see Drent et al., 2003 for details).

For this study, 48 birds (females $N=22$, males $N=26$; adults $N=13$, juveniles $N=35$) took part in the sampling experiment and 47 of these birds (females $N=22$, males $N=25$; adults $N=12$, juveniles $N=35$) also took part in the social information use experiment. The birds were of different generations of the selection lines, and half of them were selected for slow exploratory behaviour, whereas the other half was selected for fast exploratory behaviour. We started with a selection of 55 experimentally naïve males and females born in the previous breeding season ('juveniles') and older ('adults') (exploration 0–16). One bird died before the onset of the training phase and one bird died during the training phase. The birds that were unable to learn or stopped performing the task were excluded from the experiment (five of 53). One bird died after the first experiment.

The birds were individually housed in cages (0.9 x 0.4 m and 0.5 m high) containing three perches and a water bath. The birds had ad libitum access to water and their regular food, which consisted of a homemade mixture of ground beef heart, egg, calcium and a multivitamin solution, and a commercial egg mixture supplemented with mealworms, sunflower seeds and fat balls in winter and fruit during the summer. On training and testing days the birds were deprived of live food, but on other days the birds were supplemented with mealworms. We conducted training and experiments between 0900 and 1600 hours from March to mid-June 2016 at the Netherlands institute of Ecology (NIOO-KNAW) in Wageningen. As individual housing was limited, we trained and subsequently tested the birds in two cohorts (April/May and May/June). Birds were allocated randomly to these two groups, which were similar in composition with respect to age, sex and personality.

Colour Association Task

Both experiments were based on a colour association task, in which the birds could search for rewards on a Plexiglas feeding plate (25 x 29 cm and 1.5 cm high) containing five times eight wells (Amy, van Oers, & Naguib, 2012; Titulaer, van Oers, & Naguib, 2012; see Fig. 1). Coloured felt covers attached to the plate with Velcro covered nine of these wells. The birds had to lift these covers to check whether the wells contained a reward (pieces of wax moth larvae).

Before the experiments, the birds went through a training phase to familiarize them with the feeding plate, the felt covers and the association task. Training consisted of four steps (adapted from Amy et al., 2012): (1) foraging on the plate without felt covers with rewards in three wells; (2) foraging on the plate with rewards in three wells half-covered by blue felt covers; (3) foraging on the plate with rewards in three wells fully covered by blue felt covers; and (4) training the birds to associate a specific colour (blue) by adding unrewarded black felt covers on the feeding plate. In steps 1, 2 and 3, we proceeded to the next step when the bird had taken all the rewards. To ensure all birds had associated the colour with the reward, the learning criterion during the last training step was two correct first choices out of

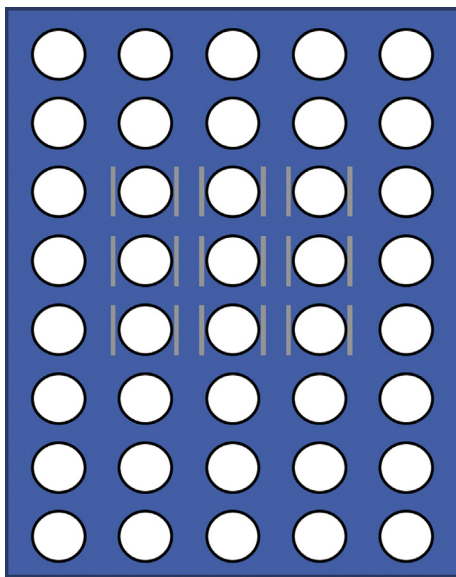


Figure 1. Schematic of the Plexiglas feeding plate with 40 wells. The grey lines next to the wells indicate the Velcro on which the felt covers of various colours could be attached.

nine options (two rewarded blue options and seven unrewarded black options) in two subsequent trials.

Experiment 1: Sampling Behaviour

The aim of this experiment was to measure to what extent an individual relies on personal information, that is, to what extent it tries known instead of novel options. In this experiment a bird was allowed to forage individually in an experimental room with four artificial trees, each having four branches (Fig. 2a). On each branch we hung a small device (5 x 3.5 cm and 1.5 cm high, Plexiglas) with a single well covered by a felt cover attached with Velcro strips (Fig. 2b).

On each tree, one of the four devices had a felt cover of the previously rewarded colour (blue), and the remaining three devices were covered in 12 different colours unfamiliar to the birds. During this experiment all options were rewarded. In advance of the experiments, we composed four combinations of one blue and three novel colours located at fixed branches within a tree. Blue was assigned to a different branch in each of the four combinations. In each trial, we randomly assigned which combination of colours would be put on which of the trees, with the limitations that the locations of the colours were different to those in the focal bird's previous trial and that the covers of the learned colour were not located on branches pointing towards each other.

The birds that reached the learning criterion in the colour association task (see above) were tested in a random order the following weekday. For the test we released a bird in the experimental room via the sliding door at the rear of this cage. From the moment the bird entered the room it was allowed to lift felt covers until it had tried a maximum of 12 different felt covers or 15 min had past. If the test subject did not lift at least five different felt covers within this time, we repeated the trial (four of 195). During the trials, the experimenter recorded the colour and location of the felt covers the focal bird lifted. We conducted four trials per individual, with at least 1 day of successful reinforcement of the colour association task between the trials. One of the 48 birds did not perform the fourth trial, making the total number of completed trials 191.

Sampling Behaviour Measure

We developed a score system to assign a measure of sampling behaviour, the 'sampling score', to each trial. Sampling was defined as the exploration of a felt cover of novel colour when the felt of the entrained colour (blue) was still present on the tree the bird was sitting on. The birds could earn bonuses or penalties depending on the colour of the felt cover lifted and on the moment of switching to another tree to lift a cover.

For each choice of a novel colour $+1/3$ point was assigned when an entrained colour was present in the same tree or $+0$ if the entrained colour in that tree was already taken. If the test bird chose to lift an entrained colour, we also took the number of novel colours still present in that tree into account: if three novel colours were present the bird was assigned -1 point, if two novel colours were present $-2/3$, if one novel colour was present $-1/3$ and if no colours were present $+0$. Additionally, if a bird switched trees when there was still an entrained colour present $+1$ point was assigned, and if there were three, two or one novel colours present the bird was assigned -1 , $-2/3$ or $-1/3$ point, respectively. If the bird did not switch trees after sampling a felt cover no points were assigned. Minimum sampling corresponded to first lifting all covers of the learned colour giving a sampling score between -7 and $-11^{2/3}$ (minimum and maximum penalty assigned by switching trees, respectively). If a bird sampled maximally, that is, only picking

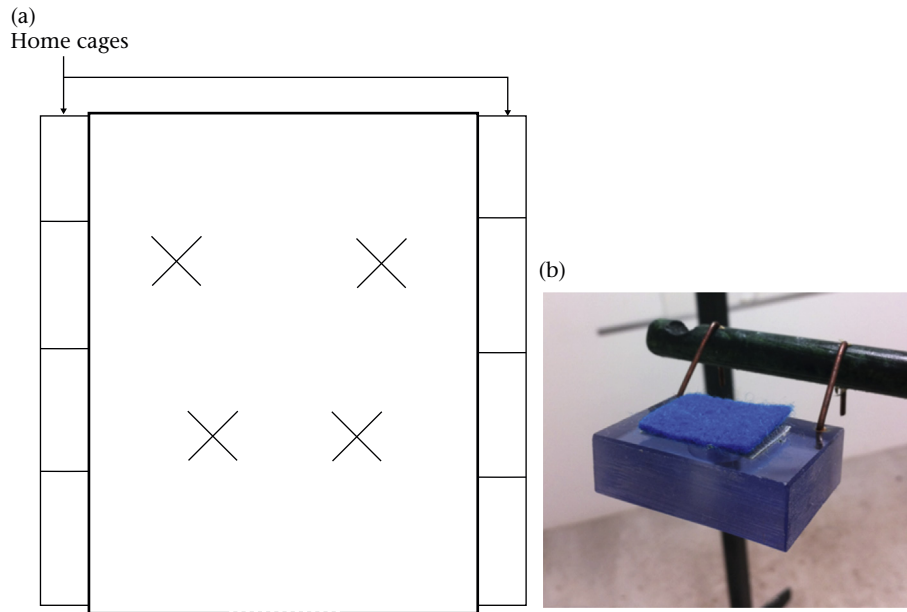


Figure 2. Set-up of the sampling behaviour experiment. (a) Schematic of the set-up of the experimental room. The dashed line indicates the one-way screen from which the experimenter was able to observe. The crosses depict artificial trees. (b) Picture of the experimental device, with one well covered by a felt cover, hanging on the branch of an artificial tree. Four such devices were present on each experimental tree.

Covers in tree	Lift entrained colour	Lift novel colour	Switch trees				
<table border="1"><tr><td>E</td><td>N</td></tr><tr><td>N</td><td>N</td></tr></table>	E	N	N	N	-1	+1/3	
E	N						
N	N						
<table border="1"><tr><td>E</td><td>N</td></tr><tr><td>N</td><td></td></tr></table>	E	N	N		-2/3	+1/3	+1/3
E	N						
N							
<table border="1"><tr><td>E</td><td>N</td></tr></table>	E	N	-1/3	+1/3	+2/3		
E	N						
<table border="1"><tr><td>E</td></tr></table>	E	0		+1			
E							
<table border="1"><tr><td>N</td><td>N</td></tr><tr><td>N</td><td></td></tr></table>	N	N	N			0	-1
N	N						
N							
<table border="1"><tr><td>N</td><td>N</td></tr></table>	N	N		0	-2/3		
N	N						
<table border="1"><tr><td>N</td></tr></table>	N		0	-1/3			
N							

Figure 3. Overview of the sampling score system. On the left-hand side are the colours (E = entrained, N = novel) still present in the tree in different scenarios. Numbers indicate the bonuses or penalties earned by a bird lifting a felt cover of the entrained colour or a novel colour or switching trees.

novel colours, it gained a sampling score between +7 and +11²/₃ (minimum and maximum points earned by switching trees, respectively; see Fig. 3).

To verify our way of quantifying sampling behaviour, we generated 1000 random sampling scores by randomly choosing five

to 12 times from all possible options consisting of a colour (learned or novel) and a tree (tree number 1, 2, 3 or 4) that were available during the trials. We found that the number of choices did not affect the average sampling score (generalized linear model, GLM: number of choices: $F_{992,7}=1.105$, $P=0.36$), but it did affect the

variation in sampling score (Levene's test: $F_{992,7}=8.12$, $P<0.001$). When we excluded the birds that only made five, six or seven choices (11 of 191 trials) the variance no longer differed with the number of choices (Levene's test: $F_{624,4}=1.93$, $P=0.10$). Therefore, we chose to exclude the trials in which the birds made fewer than eight choices from our analyses (remaining birds: trial 1: $N=47$; trial 2: $N=45$; trial 3: $N=44$; trial 4: $N=43$). Analyses on all trials gave similar results (see Appendix [Tables A1 and A2](#) for an overview).

Experiment 2: Social Information Use

We presented social information to the test subjects by playing videos of a conspecific, a novel method that has previously been used successfully to present social cues to birds (e.g. [Bird & Emery, 2008](#); [Hämäläinen et al., 2017](#); [Ophir & Galef, 2003](#)), including great tits ([Snijders, Naguib, & Van Oers, 2017](#)). On these videos the bird lifted covers from the feeding plate also used in the colour association task ([Fig. 1](#)). The demonstrating bird was an adult male that was neither related to nor familiar with (i.e. housed in the same group in the months before the experiments) any of the test subjects. We recorded 12 videos of this bird lifting felt covers of one particular colour to obtain rewards. In each of these videos nine felt covers (three covers of three different colours) were attached to the feeding plate. In total, we used 12 unique rewarded colours in the videos; each colour was used as the rewarded colour in one video and as an unrewarded colour in two other videos. One colour could only appear once in the videos in combination with another colour and we did not use the colour (blue) the test birds were trained on during the sampling experiment.

The demonstrating bird was recorded in its home cage from 0.3 m away using a Panasonic HC-V550 Full HD camcorder (AVCHD, 1920 x 1080 pixels, 25 frames/s). We edited the videos using iMovie (Apple iMovie 9.0.9) to minimize the time the bird spent out of frame, to cut out touches of an unrewarded colour, to remove the sound and to loop the video three times. The final length of the videos was between 1 min 56 s and 4 min 18 s (see Video in the online version for an example of the videos).

Supplementary material related to this article can be found online at <https://doi.org/10.1016/j.anbehav.2019.02.002>.

We showed each focal bird all 12 videos on 12 consecutive weekdays, one video per day. We prepared 10 different sequences of videos, in which two consecutive videos never contained the same colours, to minimize the possible carryover effects of previous experience with the colours, and randomly assigned these sequences to the birds. The videos were played on an LCD monitor (HP E231 23 inch, 1920 x 1080 pixels, 60 Hz, 250 cd/m²) placed 0.3 m from the home cages.

After the playback of the video, we removed the monitor and placed a feeding plate with the same colours on the same locations as shown on the video, but now unrewarded, in the cage. While observing the focal bird we noted the first cover it lifted and we removed the plate from its cage immediately afterwards. If the bird did not lift a felt cover within 10 min, we aborted the trial and noted that the bird did not choose (54 of 564 trials). In the afternoon of test days 4 and 8 the birds were reinforced by means of placing an experimental device in the home cages containing rewards covered by three felt covers of the learned colour (blue). We did this to retain motivation for solving the task. We did not observe a substantial effect of the reinforcement on the copy ratio of the following test (copy ratio = number of copied choices divided by the total number of choices per bird, range 0.26–0.49), which was 0.04 and 0.05 lower on the test days directly following reinforcement).

Data Collection and Statistical Analysis

We tested our hypotheses by running linear models (Gaussian distribution with identity link function) and binomial GLMs (quasibinomial family and logit link function) using the lme4 package (version 1.1-14, [Bates, Mächler, Bolker, & Walker, 2014](#)) in R (version 3.4.1, [R Core Team, 2017](#)). We included age (juvenile or adult), sex and body condition as control variables in all models, since these could influence personal and social information use ([Aplin, Sheldon, & Morand-Ferron, 2013](#); [Rockwell, Gabriel, & Black, 2012](#)). For body condition, we used the standardized residuals from a linear regression of mass on tarsus length, corrected for sex and date of weighing ([Green, 2001](#); [Schulte-Hostedde, Zinner, Millar, & Hickling, 2005](#)). Age, sex and body condition were not found to be significant (all $P>0.1$), but we kept them in our models. We confirmed normality of data and of model residuals by visual inspection of QQ plots and assessed equality of variance using Levene's test. We created graphs using the ggplot2 package ([Wickham, 2009](#)). During all experiments the experimenter was unaware of the exploration scores of the test subjects.

To assess whether birds used information in the sampling behaviour experiment, we compared sampling scores of the randomly generated data with scores obtained during tests by conducting Welch's two-sample t tests. We calculated repeatability (range 0–1, closer to 1 indicates highly repeatable) and corresponding confidence intervals (CI) of the normalized sampling score using the rptR package ([Nakagawa & Schielzeth, 2010](#); [Stoffel, Nakagawa, & Schielzeth, 2017](#)). We assessed the influence of exploration on sampling score per trial by running linear models (LM) with sampling score as the response variable, and over all trials by running linear mixed models (LMM) by adding trial number as a fixed factor and bird ID as a random intercept effect. To investigate social information use, we first compared the copy ratios to $1/3$ (expected copy ratio if the birds chose randomly) using a two-sided one-sample t test. To test whether individuals with different exploration scores differed in their copy ratio, we used a binomial GLM with the number of copied and noncopied choices combined as the dependent variable. We tested for significance of fixed effects by comparing the model with and without the factor of interest.

Ethical Note

We chose to deprive the birds only of live food and not all their food before the training and trials, since there are indications for a link between personality and metabolic rate ([Bouwhuis, Quinn, Sheldon, & Verhulst, 2014](#); [Mathot, Godde, Careau, Thomas, & Giraldeau, 2009](#)). Complete food deprivation could therefore have resulted in differences in motivation between the personality types, which could have biased our results. All experiments were approved by an ethical committee (DEC-KNAW licence no. NIOO 14.12 to KVO) and daily health checks were carried out to ensure the birds' welfare. Birds returned to the stock population after the behavioural experiments.

RESULTS

Sampling Behaviour

To test whether overall the birds paid attention to the colours when choosing, we compared the sampling scores of the test subjects with the randomly generated sampling scores (mean=0.44, 95% CI [0.25;0.63]). We found that, overall, birds sampled fewer devices than expected by chance (mean=-0.61, Welch's two-sample t test: $t_{71,15}=4.71$, $P<0.001$). This was also apparent when looking at trials 3 and 4 (trial 3: mean=-1.07,

$t_{50,50}=4.03$, $P<0.001$; trial 4: mean=-1.32, $t_{47,76}=4.14$, $P<0.001$), but not when looking at the first two trials (trial 1: mean=0.29, $t_{51,26}=0.55$, $P=0.59$; trial 2: mean=-0.36, $t_{47,94}=1.78$, $P=0.08$). We found a low but significant repeatability of sampling score across the trials of 0.015 (95% CI [0.00;0.14]).

We decided to carry out our analyses on sampling scores in trial 4, since there it was significantly different from random and the birds had the most time to get used to the set-up. Sampling score increased by $0.32 (\pm 0.1 \text{ SE})$ per exploration score, corresponding to more personal information use in slower than faster exploring individuals (GLM: exploration: $F_{39,4}=10.35$, $P=0.003$; Fig. 4). Running this analysis using the mean sampling score over all four trials showed a similar effect (GLMM: exploration: $\chi^2=3.74$, $P=0.05$, estimate = $0.10 \pm 0.05 \text{ SE}$).

Social Information Use

With an average copy ratio of 0.38 [95% CI 0.34;0.42], the birds overall used more social information than expected by chance (one-sample t test: $t_{46}=2.26$, $P=0.03$). The copy ratio decreased with exploration (estimate $-0.051 \pm 0.024 \text{ SE}$), indicating that slower individuals used more social information (GLM: exploration: $\chi^2=4.83$, $P=0.009$; Fig. 5).

Personal versus Social Information

When combining the results of our two experiments, we can infer that slower exploring individuals rely more on available personal and social information when making decisions, whereas faster explorers use less or no prior information (see Fig. 6).

DISCUSSION

We examined whether personal and social information use are related to personality by testing great tits in two experiments. Slow explorers relied more on personal information when making decisions, whereas the fast explorers relied less on prior knowledge.

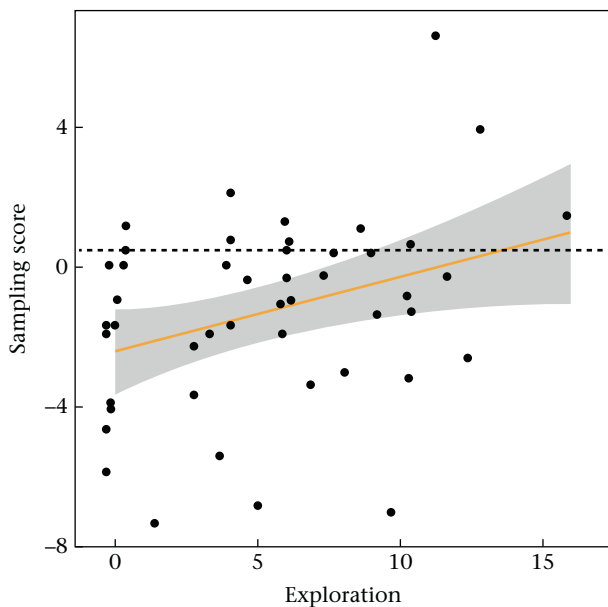


Figure 4. Association between exploration and sampling score in trial 4 ($N=47$); a lower sampling score indicates more personal information use. The dashed line indicates the mean sampling score as a result of random choices (0.43); the shaded area around the regression line indicates the 95% confidence interval.

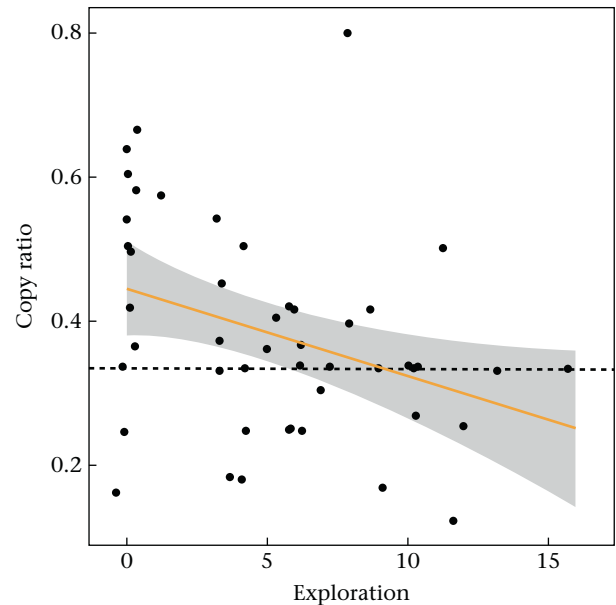


Figure 5. Association between exploration and the use of social information (copy ratio, the number of copied choices divided by the total number of choices per bird; $N=47$). The dashed line indicates the copy ratio as a result of random choices ($1/3$); the shaded area around the regression line indicates the 95% confidence interval.

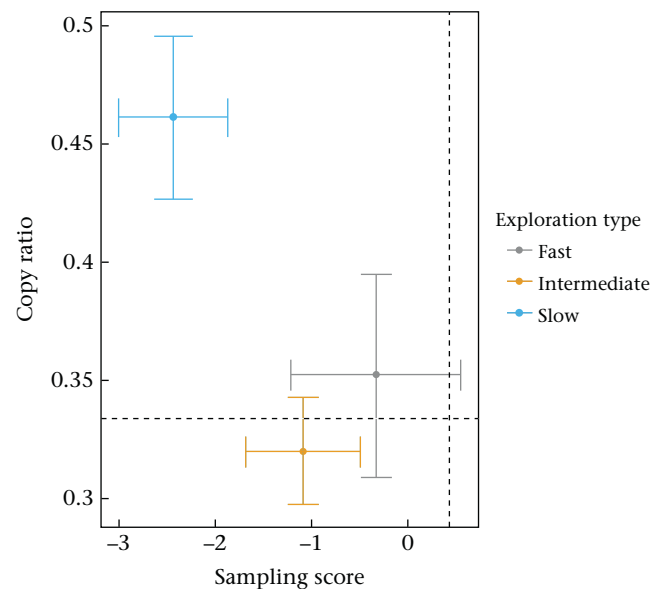


Figure 6. Mean copy ratio (number of copied choices divided by the total number of choices per bird) and mean sampling score in trial 4; more negative values indicate higher use of personal information. Birds are grouped into three exploration types for visualization purposes: slow (exploration=0–3, $N=17$), intermediate (exploration=4–7, $N=16$) and fast (exploration=8–16, $N=14$) explorers. The dashed lines indicate values of random decisions (0.43 for sampling score, $1/3$ for copy ratio); error bars depict standard errors of the mean.

We also showed that slower explorers used more social information provided by a video playback of a conspecific. Our study shows that slow explorers base their behaviour more on prior knowledge of both personal and social origin, whereas fast explorers tend to act less according to available information.

Our finding that slow-exploring birds tend to rely on personal information more than fast-exploring birds was contrary to our predictions. We expected the fast-exploring birds to stick more to

their personal knowledge, since previous studies in captive great tits found that, after the location of food was changed, the fast explorers kept visiting the previous location, while slow explorers tended to change their behaviour faster (Drent & Marchetti, 1999; Verbeek et al., 1994) and were also found to take longer to form the routine of only visiting one kind of feeder (Drent & Marchetti, 1999). A recent study in wild great tits, however, has found that when previously rewarded food patches were no longer rewarded, slower exploring great tits sampled these empty food patches more instead of sampling novel food patches (Arvidsson & Matthysen, 2016). This is in line with our finding that slower explorers went back to the previously rewarded options, a difference being that in our experiment the previously rewarded options were still rewarded. Here we have demonstrated that, even when personal knowledge is the same for all individuals and remains correct, personality types differ in whether they act upon this information or sample novel options instead.

We also showed that slower explorers not only relied more on personal information, but, in line with our predictions, used more social information than fast explorers as well. This result supports an earlier study in which barnacle geese were able to observe a foraging and nonforaging demonstrator pair, before choosing which of the pairs to approach to find food (Kurvers et al., 2010). There, shyer barnacle geese were also found to more often choose according to the social information than bolder individuals. In that study and in ours the effects of sociability, that is, the tendency to approach or avoid conspecifics, was minimized since the birds were unable to approach the demonstrator, and consequently all birds had access to the same social information. Our study demonstrates that when all individuals have the same social information, faster exploring great tits use it less.

To understand why fast- and slow-exploring animals vary in information use, it is crucial to decompose information use into distinct processes, that is, the acquisition, application and exploitation of information (Carter, Torrents Ticó, & Cowlshaw, 2016). The acquisition of information is related to how an individual moves through, and pays attention to, the environment, while the application involves incorporating information into behavioural decisions. The exploitation of information signifies how successful an individual is in gaining benefits from applying information. Each of these processes might involve distinct cognitive capacities, indicating that individuals might experience different costs or constraints at each level (Carter et al., 2016). The limitations operating at each level could be linked to individual characteristics, such as dominance, age and sex, but also to personality (Carter, Marshall, Heinsohn, & Cowlshaw, 2014).

In our study we examined the processes of acquisition and application of information in different personality types. In our first experiment we measured whether birds decided to apply personal information or to obtain novel information by sampling the environment instead. Because all birds reached a learning criterion prior to testing we assumed that the birds had obtained similar personal information, and therefore we have shown in this study that personality types differ in their tendency to apply this personal information.

In our experiment on social information use we presented social information to the birds and measured whether they chose according to this information, thereby not separating the processes of acquiring and applying information. Therefore, it could be that slower explorers obtained more social information as a result of paying more attention to the demonstrator (e.g. Van Oers et al., 2005). Alternatively, both personality types obtained the same social information, but slower explorers had a higher tendency to adjust their behaviour to this information, whereas faster explorers tended to ignore this knowledge. The collection of social information

might not always correlate with its usage (e.g. Carter et al., 2014), and therefore quantifying the collection of social information, as, for example, time spent watching a video screen (Hämäläinen et al., 2017), could have shed light on these two mechanisms.

It would also be interesting to study personality-related differences in the last process of information use, the exploitation of information, which our experiments in a captive setting with individual birds did not allow us to do. Earlier research has shown that slow great tits seem to have a lower competitive ability than fast explorers (Cole & Quinn, 2012), which might influence to what extent individuals exploit information. To take competitive ability and, for example, social network position (Carter et al., 2014) into account, the exploitation of information should be tested in a social context, ideally in the wild.

Combining the results of both our experiments shows that slower explorers rely more on information from both personal and social origin, indicating personality-dependent variation in the incorporation of information of any source. Indeed, there is evidence not only that individuals are limited in their behavioural flexibility, but also that the level of flexibility differs between individuals within species (Coppens et al., 2010). Our study supports the hypothesis that there is individual variation in the extent to which animals are behaviourally flexible with respect to incorporating information into their behaviour and indicates that slow-exploring animals are more flexible in this respect (reviewed in Coppens et al., 2010; Mathot et al., 2012).

Underlying our findings might be personality-dependent constraints and payoffs of using both types of information, possibly related to cognition. Personality types seem to employ different cognitive styles, for example regarding the speed–accuracy trade-off (Sih & Del Giudice, 2012). Fast explorers are thought to prefer speed to accuracy, while the opposite is true in slow-exploring individuals (Sih & Del Giudice, 2012). These cognitive styles might pose constraints on the flexibility of the speed–accuracy trade-off, causing slow explorers to move through the environment slower while relying more on prior knowledge and fast explorers to be less accurate in applying information and consequently sample the environment more.

By adopting different information use strategies, the personality types experience different risks and rewards in coping with environmental uncertainty. Relying on information is a safer strategy than sampling the environment, but might incur (cognitive) costs of incorporating information into behaviour (Wolf, van Doorn, & Weissing, 2008). Therefore, an alternative strategy could be not to act according to previously obtained information and instead sample the environment. Faster exploring great tits are known to be more risk prone (Van Oers et al., 2005), which can be related to a higher tendency to take the risk of sampling the environment instead of sticking to information from a personal or social origin. In this way the strategy of more exploratory individuals could result in higher rewards, since they might find and exploit novel resources earlier. More exploratory wild blue tits, *Cyanistes caeruleus*, for example, were found to discover feeders faster than less exploratory conspecifics (Herborn et al., 2010).

The payoffs of the different information use strategies are not fixed but vary with environmental context. In a more variable or higher quality habitat it might be more beneficial to take the risk to ignore prior knowledge and sample the environment to find new resources. In more constant or resource-scarce environments, however, it might be better to play safe and stick to prior knowledge. Blue jays, *Cyanocitta cristata*, for example, have been shown to use more personal and social information in predictable environments, while their reliance on prior information, especially of social origin, decreases in less predictable environments (Heinen & Stephens, 2016). The variability of available

resources in an environment might therefore influence the pay-offs of the information use strategies, and thereby populations in different environments might vary in their composition with respect to personality types (Mathot et al., 2012). For example, urban populations of blackbirds, *Turdus merula*, have been found to be more neophobic than rural populations (Miranda, Schielzeth, Sonntag, & Partecke, 2013), and blue tits in pine-wood forest seem to be less exploratory than in oakwood forest (Serrano-Davies, Araya-Ajoy, Dingemanse, & Sanz, 2017). The features of habitats might favour one information use strategy over the other, consequently influencing the prevalence of the different personality types.

Furthermore, the prevalence of information use strategies might depend on the social context. The payoffs of the two strategies in a population could be frequency dependent, since animals that rely more on information might rely on others that sample the environment to obtain that information. Therefore, there needs to be a balance in the discovery of novel information and the spread of this knowledge. The ratio in which the two information use strategies are in equilibrium might be when they both have the same payoffs. This is also reflected in studies on 'producer–scrounger games' in which searching for resources ('information producing') and exploiting investments of others ('information scrounging') are two strategies (Barnard & Sibly, 1981). These strategies are in equilibrium in a producer–scrounger ratio in which the payoffs of both strategies are equal (Barnard & Sibly, 1981).

In conclusion, we have shown that personality types differ in the use of personal and social information. Slow-exploring animals adopt a safer strategy by relying more on personal and social information, while fast-exploring animals tend to sample more novel options and have the potential to obtain higher rewards. The prevalence of these different information use strategies across personality types implies personality-related costs and constraints in using information. To our knowledge, this is the first time that the relation between personality and personal and social information use has been studied in two separate experiments, allowing us to draw conclusions about how personality types differ in their strategies to cope with environmental uncertainty when either personal or social information is available. Our results might contribute to understanding variation in the prevalence of personality types across different environment contexts, thereby providing support for an ecological explanation of the existence of personality.

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APPENDIX

Table A1

Comparison of birds' sampling scores with the randomly generated sampling scores (using Welch's two-sample *t* test) with data of all the birds

Trial	Mean	<i>t</i>	<i>df</i>	<i>P</i>
All	-0.62	4.63	70.71	<0.001
1	0.29	0.36	52.40	0.72
2	-0.36	1.77	51.78	0.08
3	-1.07	4.51	56.28	<0.001
4	-1.32	4.27	51.74	<0.001

Table A2

Generalized linear models investigating the relation between exploration and sampling score with data of all the birds

Response variable	Explanatory variable	Test statistic	<i>df</i>	<i>P</i>	Estimate ±SE
Sampling score (trial 4)	Exploration	$F = 7.61$	42,1	0.009	0.26 ± 0.10
Sampling score (all trails)	Exploration	$\chi^2 = 4.05$	1	0.044	0.10 ± 0.05

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