Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc



Personality and problem-solving in common mynas (*Acridotheres tristis*)



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ARTICLE INFO

Article history: Received 18 March 2016 Received in revised form 23 September 2016 Accepted 30 September 2016 Available online 4 October 2016

Keywords: Cognition Exploration Personality Problem solving

ABSTRACT

Animals show consistent individual differences in behaviour across time and/or contexts. Recently, it has been suggested that proactive personality types might also exhibit fast cognitive styles. The speed with which individuals sample environmental cues is one way in which correlations between personality and cognition might arise. Here, we measured a collection of behavioural traits (competitiveness, neophobia, neophilia, task-directed motivation and exploration) in common mynas (*Acridotheres tristis*) and measured their relationship with problem solving. We predicted that fast solving mynas would interact with (i.e. sample) the problem solving task at higher rates, but also be more competitive, less neophobic, more neophilic, and more exploratory. Mynas that were faster to solve a novel foraging problem were no more competitive around food and no more inclined to take risks. Unexpectedly, these fast-solving mynas had higher rates of interactions with the task, but also displayed lower levels of exploration. It is possible that a negative relation between problem solving and spatial exploration arose as a consequence of how interindividual variation in exploration was quantified. We discuss the need for greater consensus on how to measure exploratory behaviour before we can advance our understanding of relationships between cognition and personality more effectively.

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1. Introduction

It is now well established that many animals show among individual differences in behaviour that are consistent across time and/or contexts (Bell, 2007; Biro and Stamps, 2008; Sih et al., 2004; Stamps, 2007 typically referred to as personality (Sih et al., 2004) or temperament (Réale et al., 2007). Several axes of inter-individual behavioural variation have been identified, including aggression, activity, sociality, exploratory tendency and risk responsiveness (Réale et al., 2007). Inter-individual variation along these distinct axes can be correlated across multiple (two or more) contexts, in which case, the term behavioural syndrome is used (Sih et al., 2004. 2005). For example, individuals that are more aggressive in competitive contests might also be bolder in the presence of a predator (Bell and Sih, 2007). Réale et al. (2010) went on to propose the concept of 'pace-of-life' syndrome, whereby suites of correlated axes might be organised along a continuum from fast, proactive (aggressive, bold, asocial and active) to slow, reactive (non-aggressive, shy, social and inactive).

A more recent development in the field is the suggestion that inter-individual variation in personality might be related to interindividual variation in cognition (Carere and Locurto 2011; Griffin et al., 2015; Sih and Del Giudice 2012). Sih and Del Giudice (2012) proposed the first integrated framework for this relationship by considering jointly how individuals might fall simultaneously along both personality and cognition axes of variation. This included the notable introduction of the concept of cognitive style to the non-human animal literature to refer to a consistent tendency to trade off speed against accuracy in learning, memory, information sampling, impulsivity and decision making (Sih and Del Giudice, 2012). For example, individuals with a 'fast' cognitive style might make decisions consistently more quickly, but consistently less accurately, than individuals with a 'slow' cognitive style (Sih and Del Giudice, 2012). Similarly, individuals with a fast cognitive style might tend to be less discriminatory and therefore less choosy (e.g. in mate choice experiments) than individuals with a slow cognitive style. Sih and Del Guidice (2012) inrated the idea of cognitive style with that of personality by suggesting that individuals with fast cognitive styles might also display fast, proactive personalities, whereas those with slow cognitive styles might be characterised by slow, reactive personalities.

The speed with which individuals encounter environmental cues is one way in which correlations between cognition and personality might arise (Sih and Del Giudice, 2012). Animals with proactive personalities are generally considered to explore their environments quickly, and to be more bold, more willing to take risks, and more aggressive (Koolhaas et al., 1999; Réale et al., 2010). In contrast, individuals with reactive personalities explore novel environments less quickly, are more shy, less willing to take risks and less aggressive (Koolhaas et al., 1999; Réale et al., 2010). Therefore, proactive personalities will tend to encounter new information at faster rates than reactive individuals. As a consequence, proactive individuals might learn about new environmental contingencies more quickly in absolute time than reactive individuals simply because they encounter new or altered environmental contingencies more frequently per unit time (Griffin et al., 2015; Griffin and Guez 2016).

Innovative problem solving, or just problem solving, typically involves measuring performance on novel problems, from manipulating objects to negotiating mazes to gain access to food or other desirable objects (Cauchard et al., 2013; Keagy et al., 2009) (reviewed by Griffin and Guez, 2014, 2016). Positive correlations between performance on problem solving (e.g. solving latencies and probabilities) and learning (e.g. acquisition speeds and accuracies) tasks have lead some authors to suggest that inter-individual variation in problem solving provides a measure of inter-individual variation in cognition (for a detailed review, see Griffin and Guez, 2016). For example, feral pigeons (Columba livia) that were faster to solve a puzzle box to reach an enclosed food item also acquired an alternative extractive task in fewer social demonstration trials (Bouchard et al., 2007). In another example, European starlings (Sturnus vulgaris) that were the first to solve a novel foraging problem in a group foraging context also progressed more rapidly through successive stages of a shaping procedure to perform a novel foraging technique (i.e., remove a lid from a container to access a mealworm reward). Difficulties in interpreting these results have been discussed in detail by Griffin and Guez (2016) and are not discussed further here. However, the recent finding that great tits (Parus major) that solved a novel foraging task in captivity (leverpulling) acquired an operant learning task (colour discrimination) in the wild in fewer trials than non-solvers (Morand-Ferron et al., 2015) suggests that, at the very least, variation in problem solving tendency can be used as a correlate of variation in cognition (Griffin and Guez, 2016). In this case, problem solving provides a means of examining cognition-personality relationships. This was the aim of the present study.

We explored the relationships between inter-individual variation in problem solving and neophobia (risk taking), attraction to novelty, competitiveness, and exploration using wild caught, captive tested common mynas, one of the world's most successful avian invaders. Common mynas (Acridotheres tristis) have been subject of a substantial body of research on problem solving and learning (Griffin et al., 2013). Hence, they provide an excellent opportunity to examine relationships between problem solving and personality. Rather than restricting our analysis of problem solving performance to latencies and/or probabilities, as has been the case in much work on problem solving to date, we also measured how frequently individuals interacted with the problem-solving task and related this measure to our measures of personality. By quantifying how frequently the subject makes contact with, and therefore samples information about the task at hand, attempt rate provides a measure of task-directed motivation (Griffin and Guez, 2014). The measure is known to be repeatable across different problem solving tasks in common mynas (Griffin and Diquelou, 2015). We predicted that faster problem solvers would be those that engaged more with the problem-solving task and that these individuals would show fast, proactive personalities, including low neophobia, high neophilia, high level of competitiveness, fast exploration. This is because these personality traits are likely to facilitate faster sampling of environmental information.

Finally, to ensure that neophobia, attraction to novelty (neophilia), competitiveness and exploration were repeatable across time, all behavioural traits were measured on two consecutive occasions.

2. Methods

2.1. Subjects & husbandry

Forty-nine common mynas were caught from the wild in the city of Newcastle and surrounding suburbs using a trap specifically designed to trap this species (for details see Griffin, 2008). Birds were transported to the Central Animal House of the University of Newcastle, where they were weighed, measured (tarsus, beak and wing) and individually marked with coloured plastic leg bands. Adults were distinguished from juveniles based on their brownish plumage (Counsilman, 1974). Mynas are not sexually dimorphic, so subjects were sexed using a DNA analysis sampled in feathers (http://dnasolutions.com.au/product-category/dna-tests/ animal-dna-testing/). Birds were left undisturbed in outdoor quarantine aviaries (1.95 m \times 2.2 m \times 1.0 m) with food (dog pellets) and water ad libitum, for a minimum of seven days to be treated for internal parasites and to further acclimatize to captivity before testing began. As the number of birds captured per unit time was not under our control and only a subset of birds could be tested at any one time, time in captivity prior to testing varied across birds. Common mynas acclimatize quickly to captivity so we do not think that responses changed beyond the minimum acclimatization period. In addition, each individual underwent one week of acclimatization after being moved into experimental housing.

For testing, birds were moved from quarantine aviaries to outdoor experimental aviaries $(1.95 \, \text{m} \times 2.2 \, \text{m} \times 1.0 \, \text{m})$. The aviaries were positioned in a circle to allow acoustic and distant visual contact, but were far enough apart to ensure that no social learning occurred during tests. These conditions are known to facilitate acclimatization of wild-caught mynas to captivity (Griffin, 2008). Each aviary was equipped with tree branches, perches, a nest box, a water bath, and food and water dishes. Birds were provided with ad libitum access to water and food throughout the testing period, except prior to some tests that required overnight food deprivation.

2.2. General procedure

In order to create groups of birds whose members were unfamiliar with each other, group members were drawn randomly from different quarantine holding aviaries. In order to maximise the use of all trapped birds, our final groups included four groups of five adult males, two groups of five adult females, one group of four adult females one group of five juvenile males, one group of five juvenile females and one mixed group of adults (4 males and 1 female). In creating groups with a standard social structure, we attempted to avoid known effects of male over female, and adult (large body size) over juvenile (small body size) dominance in common mynas (Griffin et al., 2013). Each group was given ad libitum access to food and water and left for one week to acclimatize to their new physical and social environment. Each group was then tested following the same procedure over a two-week period (Weeks 1 and 2).

During week 1, each individual's competitiveness around food within its group was measured on two consecutive mornings (Fig. 1). Then at the end of the week, each myna group was split and each individual placed alone in an outdoor test aviary (Fig. 1). During week 2, following two days of acclimatization, each bird undertook two different problem-solving tests on days 1 and 2 of testing. On day 3, each bird underwent a neophobia test in the morning and neophilia test in the afternoon. This procedure was repeated on day 4. On the morning of day 5, each bird was moved to a small indoor individual cage (50 cm \times 50 cm \times 60 cm; W \times H \times D). From there, it participated in one exploration test a few hours after being moved, and a second exploration test the following morning (day 6). During tests in outdoor aviaries, focal mynas were filmed

from behind an observation hide placed 6 m away. During exploration tests, the focal bird was filmed remotely. Two birds escaped during the transfer from outdoor aviaries to small cages, so only forty-seven birds participated in the exploration tests.

At the end of testing, mynas were moved back into large group flight aviaries where they were held for the purposes of taking part in other ongoing studies. All procedures were approved by the ethics committee of the University of Newcastle A-2011-154.

2.3. Behavioural tests

2.3.1. Competitiveness

The night before each test, groups of five birds were food deprived from sunset to sunrise. Early next morning, dog pellets were offered in one small feeder container such that only one bird could feed at any given moment. To reduce any neophobic response, the feeder containing food had been placed in the aviary for two full days prior to testing, as well as on the night before the test, but with no food in it. Dog pellets were crushed so that mynas could only consume a very small amount of food at each peck. In this way, individuals had to remain at the feeder for longer periods or come back several times to get a sufficient quantity of food (Aplin et al., 2013; Bouchard et al., 2007; Cole et al., 2012). Each group was videorecorded for one hour following the introduction of the feeder.

Using this setup, we quantified each individual's competitive tendency by sampling both an individual's propensity to compete for access to food ('competitiveness', Boogert et al., 2006) and its propensity to behave aggressively towards conspecifics ('agonistic behaviour', Boogert et al., 2006). Time spent at the feeder (total time (1) and percentage (2)), priority access to the feeder (3) (order of landing at the feeder: 1 to 5), and number of visits to the feeder (4) were measured to evaluate each bird's competitiveness, while displacements (5) were measured to obtain a measure of each bird's agonistic tendency (Boogert et al., 2006). Displacements were scored each time a bird provoked the movement of a conspecific away from the feeder by pecking it, threatening it with aggressive postures (e.g. bill opened or all body tense toward the other bird) or approaching it. Only when an aggressive act was followed by withdrawal of the targeted conspecific, a displacement was scored. A Principle Component Analysis (with varimax rotation) was conducted to determine whether the collection of the five behavioural variables sampled during the competitiveness test could be reduced to a smaller number of factors that captured an individual's propensity to compete in a social context and could be related to performance on other tasks (Tabachnick and Fidell, 1996). PC-scores were constructed using the correlation matrix. Within each group of five birds, the competitive scores were ranked and each bird received a number from one (most competitive) to 5 (least competitive). This group-based competitive rank was used to examine whether a myna's competitive position within a social group predicted problem-solving performance.

2.3.2. Problem solving

During problem-solving tests, each bird was presented with two out of four possible different novel extractive foraging tasks, which were presented in a random order across two successive days (Fig. 1). Tasks were counterbalanced across birds such that equal numbers of birds underwent each of the four tasks during the problem-solving first test, as well as each of the four tasks during the repeat test. By sampling problem solving across a variety of tasks, we attempted to establish more general, rather than task-specific, relationships between problem solving and personality. The first two possible tasks consisted of a Petri dish (100 mm \times 15 mm) with either an inverted, or an upright, lid. The inverted lid could only be lifted by grabbing a hook attached

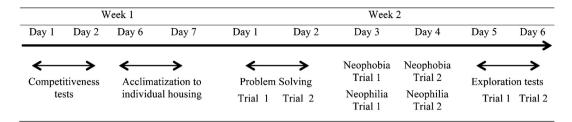


Fig. 1. Chronological order of behavioural testing. The two depicted weeks of testing were preceded by one week of acclimatization to experimental housing (see Subjects & husbandry).

Problem solving: Trials 1 and 2 indicate that birds encountered 2 different tasks (puzzles).

Neophobia & Neophilia: Trials 1 and 2 indicate that birds encountered 2 different novel objects.

to its centre, while the upright lid could be removed by either leveraging it upwards, or grabbing a piece of tape attached to its edge. The third possible task consisted of a Styrofoam coffee cup (2.9 cm \times 1.8 cm \times 2.9 cm; L \times W \times H) glued to a small wooden board. The cup was covered with a Petri dish lid, which was glued into place so it could not be removed, but allowed visual access to the food inside the cup. One 3 cm diameter hole in the side of the cup was covered in transparent plastic film, which needed to be pierced to access the food. The fourth task consisted of a piece of paper that needed to be pulled out of a plastic champagne flute (130 ml capacity, 53 mm top/171 mm height) to access the food (for task illustrations, see Griffin et al., 2013). To reduce any neophobic responses, the apparatus was placed with an available dog pellet in the aviary the evening before the test. The dog pellet was placed on the lid of the cup, on the floor against the entrance of the flute, and inside the open Petri dish. To be sure birds did not practice motor actions necessary to solve the task, lids were removed from the Petri dishes and the piece of paper was added to the cup only for the test.

The problem-solving test was then conducted early in the morning following overnight food deprivation. To begin the test, the task was presented first with one readily available dog pellet (in the same location as the evening before the test, see above) to ensure the bird was motivated to feed. Once the focal subject had consumed the dog pellet, the experimenter approached once again from behind the hide, and placed a dog pellet inside the closed task before returning to the hide.

The total duration of each problem-solving test was 30 min (1800 s). The latency from first contact to solving the task provided a measure of problem solving performance ('solving latency'). If the focal bird did not solve, it was attributed a capped solving latency of 1800 minus the contact latency. A solving attempt was also scored as one beak-to-task or foot-to-task contact. Attempt rate was calculated by dividing the number of attempts by the solving latency. This provided a measure of task-directed motivation (Griffin and Guez, 2014).

2.3.3. Neophobia

Following overnight food deprivation, birds underwent a neophobia test early in the morning. Neophobia was evaluated by measuring the ('test') latency of the focal bird to approach a familiar food dish in the presence of a novel object and comparing it with the ('baseline') latency to approach the familiar food dish in the absence of any novel object (Griffin and Diquelou, 2015; Griffin et al., 2013; Sol et al., 2011). Objects that mynas are unlikely to have encountered in the wild were used as novel objects. Specifically, a green plastic hair brush was presented on day 1 ('test') and a pink door stop was presented on day 2 ('test repeat'). To obtain the baseline approach latency, the experimenter approached the aviary from behind a hide, and placed a dog pellet in the myna's familiar food dish, before returning to the hide. Latency to consume the food item was then measured starting from the when the bird had been

placed in the dish. If the focal myna failed to consume the food within 30 min, the test was aborted and was then attempted once again an hour later. As soon as the bird had consumed the food item and moved away from the dish, the experimenter approached the dish once again, placed dog pellets in the dish and the novel object next to it, before returning to the hide. Latency to consume the first dog pellet was measured once again, and was capped at 1800 s if the bird failed to consume the food within 30 min. A neophobia score was calculated for each bird by subtracting the baseline latency from the test latency. After testing, ad libitum food was delivered to birds for the rest of the day.

2.3.4. Neophilia

To measure attraction to novelty, an object was placed on the aviary's floor. The object was placed in a central position in the aviary, not just beside food and water so that the focal subject did not need to approach the novel object while trying to access any essential resource. Birds were then given the opportunity to explore the novel object for 30 min. Each bird was tested with two distinct objects that mynas are unlikely to have encountered in the wild, specifically an open matchbox on day 1 ('test') and an array of four small green containers on day 2 ('test repeat').

Latency to first approach the object was recorded for each bird and was capped at 1800 s if the bird failed to approach the novel object within 30 min. An approach was scored each time the bird landed or walked within 20 cm of the object.

2.3.5. Exploration

Exploration propensity was assessed in a large, unfamiliar room under artificial light with five artificial trees (Dingemanse et al., 2002) and 20 squares (58 cm \times 58 cm) painted on the room's floor (Minderman et al., 2009). Common mynas are ground foragers, so we considered important to measure tree and ground exploration. White noise was played back inside the room to mask vocalizations from caged birds in a nearby room.

Birds were housed in individual cages placed on wheels. Cages were covered with a large piece of opaque material and wheeled into the exploration room. A black curtain hanging from the ceiling covered the cage. The experimenter standing behind the cage gently lifted the opaque material, opened the cage's trap door and exited the room leaving the focal bird freely to exit the cage and explore the room. Each bird was videorecorded for 20 min after the cage had been opened. All birds exited the cage and explored the room during this time limit, except one bird that stayed in the cage for both the first and second test.

Six behavioral parameters were recorded: number of (different) trees visited, number of perches used, number of (different) squares used on the ground, total number of movements (flights, hops, walks), total number of visited places and the latency to exit the cage. A Principle Component Analysis (with Varimax rotation) was conducted to determine whether the behavioural variables could be reduced to a smaller number of factors that captured

an individual's exploratory propensity and could then be related to performance on other tasks (Tabachnick and Fidell, 1996). PCscores were constructed using the correlation matrix.

2.4. Analysis

The repeatability of the exploration and competitiveness PC scores across the two repeat tests was examined by calculating an intraclass correlation coefficient. The same coefficient was used to measure individual consistency in the latencies to 1. approach a novel object (neophilia), 2. feed next to a novel object (neophobia), and 3. solve a novel foraging problem, as well as 4. the individual consistency in task directed motivation during problem solving (attempt rate).

To determine the effects of age and sex on exploration and competitiveness, we conducted Linear Mixed Models (LMM) with test (test, test repeat), age and sex as categorical explanatory variables, as well as the two way interaction between age and sex. We included bird identity as a random factor. A compound symmetry covariance structure produced the best fit as determined by the Akaike's Information Criterion. Because neophilia and neophobia latencies included capped time values for those individuals that did not approach the novel object or feed next to a novel object, respectively, Cox proportional hazards models were used to test the effects of age and sex on these behavioural variables. This nonparametric survival framework requires few assumptions and allows the inclusion of covariates in one model for each trait while treating capped latencies (more typically death, but in this case, approach or feeding) as censored observations (Crawley, 2002). Age and sex were entered into each model as categorical explanatory variables. Latency to approach or to feed (in seconds) was entered as an outcome variable. We found latencies to be repeatable across the two repeat tests. Therefore, the mean value was used as an outcome variable in each Cox regression.

To examine the effects of age and sex on task-directed motivation, we fitted a Generalized Linear Mixed Model (GLMM) with a binomial error and a probit link function. We used number of attempts as an outcome variable with time to solve as an offset variable. We included test as a repeated measure (test (day 1), test repeat (day 2)), as well as age, sex, and their interaction, all as categorical explanatory variables. Bird identity was included as a random factor.

Finally, we examined the relationship between personality and problem solving by fitting a Cox proportional hazards model to the solving latencies and applying a backward selection technique to simplify the model. Personality measures (mean value calculated across the two tests) were entered as continuous explanatory variables, as well as attempt rate (mean value calculated across the two problem solving tests) in the full model. Age, sex and competitive rank were also entered into this model as categorical explanatory variables.

All statistical analyses were carried out using SPSS statistics 22.0 and JMP 9. Two-tailed tests were used throughout and alpha levels were fixed at 0.05.

3. Results

3.1. Behavioural traits and repeatability

3.1.1. Competitiveness

A PCA on the behavioural variables collected during each of the two competitiveness tests produced one axis with an eigenvalue greater than 1.00 explaining 57.2% (test 1) and 55.5% (test 2) of the total variation, respectively (Table 1). Variable loadings indicated that higher scores corresponded to more time spent at the

feeder, more displacements and more visits to the feeder (Table 1). Priority access to the feeder was the only behavioural variable that loaded on to a second component, but as this component had an eigenvalue <1.0, it was not considered further. Individual scores were consistent across the two tests (intraclass correlation coefficient r=0.785, P<0.001). The Linear Mixed Model did not show any significant effects of sex on exploration propensity ($F_{1,45}$ =0.074, P=0.787), age ($F_{1,45}$ =0.772, P=0.384) or their interaction ($F_{1,45}$ =0.868, P=0.357).

3.1.2. Neophobia and neophilia

Individual levels of neophobia and neophilia were consistent across the two tests (neophobia: intraclass correlation coefficient r=0.54, P=0.004; neophilia: r=0.434, P=0.026). A Cox proportional hazard model revealed no significant effect of sex, age or their interaction on neophobia (Table 2). There was also no effect of age on neophilia, but we found a significant effect of age and a significant age by sex interaction. Follow up Independent Samples Mann-Whitney-Wilcoxon test revealed that female juveniles took significantly longer to approach the novel object than juvenile males (W=15, N_(male) = N_(female) = 5, P=0.008), but this sex difference was not present in adults (W=270, N_(male) = 24 N_(female) = 15; P=0.399).

3.1.3. Exploration

The PCA on the behavioural variables sampled during each of the two exploration tests produced one component with an eigenvalue greater than 1.00 explaining 58.5% (test 1) and 57.65% (test 2) of the total variation, respectively (Table 1). Variable loadings indicated that individuals with higher scores visited more trees and perches and made more movements. Latency to exit the cage and the number of squares visited loaded onto a second component, but as these components had an eigenvalues <1.0, they were not considered further. Individual exploration scores were consistent across the two tests (intraclass correlation coefficient r = 0.733, P < 0.001). The Linear Mixed Model did not show any significant effects of sex on exploration propensity ($F_{1,43} = 0.335$, P = 0.565), age ($F_{1,43} = 2.000$, P = 0.164) or their interaction ($F_{1,43} = 1.633$, P = 0.208).

3.2. Task directed motivation

Individual levels of task directed motivation during problem solving were consistent across the two test repeats (intraclass correlation coefficient r=0.534, P=0.005). The GLMM revealed no effect of sex ($F_{4,88}$ =0.136, P=0.713), age ($F_{1,88}$ =0.001, P=0.979) or their interaction ($F_{1,88}$ =0.657, P=0.420) on attempt rate.

3.3. Predictors of problem solving

20.4% of the birds (10 of 49) solved the two tasks and 32.7% of the birds (16 of 49) solved one task. The upright Petri dish was solved by 12 birds, while the inverted Petri dish was solved by 10 birds. Cup and flute tasks were each solved by seven birds. The latencies from first contact to solving the task were consistent across the two tests (intraclass correlation coefficient r = 0.504, P = 0.008). A Cox proportional hazards model with a backward stepwise simplification revealed that exploration and attempt rate were significant predictors of problem solving (Table 3). Low exploratory birds and individuals with high attempt rates were faster to solve a novel foraging problem (Table 3; Fig. 2). The simplified model also included a significant effect of sex as well as a significant interaction of sex and age on problem solving latencies. Follow up Independent Samples Mann-Whitney-Wilcoxon tests revealed that female juveniles were significantly faster to solve than juvenile males (W = 18,

Table 1Component loadings of behaviours measured during competitiveness (N = 49) and exploration (N = 47) tests on first orthogonally rotated principal component for each test and each repeat test for each trait.

Competitiveness	Test	Test repeat	Exploration	Test	Test repeat
% time spend at the feeder	0.45	0.50	Number of trees	0.45	0.39
Priority access to the feeder	-0.37	-0.35	Number of perches	0.49	0.43
Number of visits to the feeder	0.48	0.46	Number of squares	0.34	0.31
Time spent at the feeder	0.50	0.51	Number of movements	0.39	0.48
Number of displacements	0.4	0.39	Number of visited places	0.46	0.49
			Latency to exit	-0.18	-0.29

Those variables that contribute to the biological significance of the component are indicated in bold.

Table 2 Effects of age and sex on neophobia and neophilia.

Trait	Term	Coefficient	Exp(coeff)	SE(coeff)	W	P
Neophobia	Sex (male)	-1.170	0.310	0.871	1.801	0.180
	Age (juvenile)	0.105	1.111	0.556	0.036	0.850
	Sex × Age	1.228	3.415	0.946	1.684	0.194
Neophilia	Sex (male)	-2.243	0.106	0.867	6.695	0.010*
	Age (juvenile)	-1.008	0.365	0.537	3.528	0.060
	Sex × Age	2.638	13.990	0.947	7.755	0.005**

Analyses employed a Cox regression survival analysis. For categorical covariates, hazard ratios greater than one (i.e. Exp(coefficient)) indicate an increased likelihood of solving relative to the reference category indicated in brackets, whereas hazard ratios smaller than one indicate a reduced likelihood of solving relative to the reference category. For each term, the reference category is indicated in brackets. SE: standard error.

^{**} P<0.001.

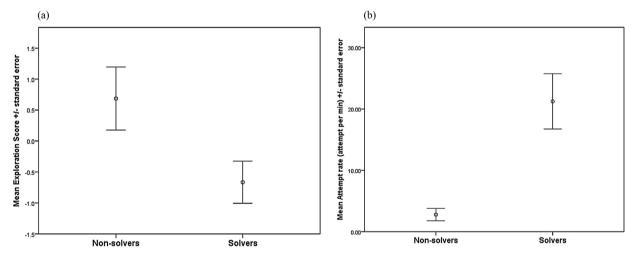


Fig. 2. (a) Association between mean (\pm SE) exploration (calculated across test and test repeat) and problem-solving success. (b) Association between mean (\pm SE) attempt rate (calculated across test and test repeat) and problem-solving success.

N(male) = N(female) = 5, P = 0.034), but this sex difference was not present in adults (W = 464, N(male) = 24 N(female) = 15; P = 0.627).

4. Discussion

This study aimed to increase our understanding of the relationships between personality, fast environmental sampling (fast exploration) and problem solving. All six behaviour performances (competitiveness, problem solving, task-directed motivation, neophobia, neophilia and exploration) were consistent across time, suggesting that these behaviours constitute repeatable individual attributes in common mynas and can be called personality traits (Boake, 1989; Réale et al., 2007). These findings extend previous work showing that task-directed motivation during problem solving (Diquelou et al., 2015; Griffin and Diquelou, 2015; Griffin et al., 2014; Perals et al. in prep.) and problem-solving performances are repeatable in mynas (Sol et al., 2012), as are neophobia (Sol et al., 2012; Perals et al. in prep.), activity and shyness (latency to exit a

nest box after human disturbance) (Perals et al. in prep.). Not only did we test each bird twice, we also modified each task slightly from the first to the second testing in order to reduce the effects of learning, habituation, and familiarisation (Dingemanse et al., 2002; Greenberg and Mettke-Hofmann, 2001). Individuals were exposed to two different objects during neophobia and neophilia tests and to two different problem-solving tasks during problem-solving tests. Finally, the spatial array of artificial trees was modified from the first to the second exploration test. Under these conditions, our tests establish not only temporal, but also some degree of crosscontextual behavioural repeatability.

Our second key finding was that task directed motivation was a strong predictor of problem solving. Individuals that made more contacts with the task per unit time were faster to solve the task; this finding is consistent with previous work showing that task directed motivation and motor diversity are systematic predictors of problem solving performance in mynas (Sol et al., 2012; Griffin and Diquelou, 2015; Diquelou et al., 2015) and other avian

^{*} P < 0.05.

Table 3Relationship between sex, age, personality and problem solving. A Cox regression was fitted to problem-solving latencies and backward simplified. The table below indicates the variables retained in the model following simplification.

Term	Coefficient	Exp(coeff)	SE(coeff)	W	P
Sex (male)	2.542	12.708	1.198	4.505	0.034*
Exploration	-0.334	0.716	0.140	5.683	0.017^{*}
Attempt rate	0.039	1.040	0.009	18.029	<0.001**
$Sex \times Age$	-3.479	0.031	1.347	6.675	0.010^{*}

The full model prior to backward simplification included sex, age, sex \times age as categorical predictor variables and exploration, neophilia, neophobia, competitive rank, and attempt rate as continuous explanatory variables. Reference categories for categorical explanatory variables (see legend Table 2) are indicated in brackets. For continuous covariates, a hazard function smaller than one indicates a reduced likelihood of solving of (1-Exp(coefficient)) for every unit increase in the predictor term. SE: standard error.

- * P < 0.05.
- ** P<0.001.

and mammalian species (Benson-Amram and Holekamp, 2012; Cauchard et al., 2013; Morand-ferron et al., 2011; Morand-ferron and Quinn, 2011; Thornton and Samson, 2012). Individual attempt rates are known to be consistent across different problem solving tasks (Griffin and Diquelou, 2015) as replicated here.

Our third key finding was that an individual's tendency to explore a novel spatial environment was the only personality trait that predicted individual variation in problem solving latency. Unexpectedly, individuals that displayed higher levels of movement through a novel space and alighted in more areas were those that took longer to solve a novel foraging problem, indicating that problem solvers were less exploratory.

Whereas Sol et al. (2012) have previously found that more exploratory individuals were more innovative, we found here that less exploratory birds were faster innovators. These two studies differ considerably in the ways in which individual exploratory tendencies were assessed, however. Whereas Sol et al. (2012) quantified the amount of object exploration during the problem-solving tests, the present study quantified each individual's propensity to move through a large novel room during a completely independent behavioural assay. Spatial exploration and object exploration do not always correlate (Fox et al., 2009; Verbeek et al., 1994). The relation found here between fast problem solvers and less exploratory birds also stands in stark contrast to the positive relationship found by Overington et al. (2011) in Carib grackles (Quiscalus lugubris). Once again, differences in methodology might come into play. Overington et al. (2011) quantified exploration by extracting a principle component axis collapsing measures of activity (movements) and exploration (different areas explored) collected upon manually releasing a bird that had just been captured in the wild into a novel space, but also latencies to feed in the presence of novel objects. When several different traits are pooled (e.g. neophobia and exploration), results become more difficult to compare across studies. The only study that has used a methodology similar to that used here (voluntary entry and movement around a novel space equipped with artificial trees) found no evidence of a relation between spatial exploration and problem solving (Cole et al., 2011). These divergent patterns highlight the need for standardised

We consider several possible explanations for why less exploratory individuals might be faster problem solvers. First, there is an ongoing discussion regarding the target trait measured in open-field tests in birds (Carter et al., 2013). Although this issue has been resolved in rodents (Koolhaas et al., 1999, 2010), in birds it is still not clear whether the test measures of an individual's propensity to gather information or emotionality. In the protocol used here, birds were not food deprived before testing and were allowed to exit their home cage freely. These methodologies are

thought to reduce stress responses and enhance information seeking behaviour (Mettke-Hofmann et al., 2002), making it more likely that we would find a positive correlation with task directed motviation and problem solving.

Another possible explanation for the relationship between low exploratory birds and fast problem solvers is that less exploratory mynas are indeed more inclined to solve novel foraging problems. The common myna is highly urbanized and found almost exclusively in close proximity to humans (Pell and Tidemann, 1997; Hone, 1976). Within this habitat, mynas can often be seen foraging on anthropogenic food sources involving packaging. More exploratory birds alighting first might have access to spilled, readily available foods. In contrast, less exploratory mynas alight later might need to manipulate the packaging to access foods remaining within the closed package, making them more apt at solving novel foraging tasks.

Finally, it is unclear to what extent assessing exploratory behaviour using the number of areas a bird alights on (high vs. low) relates to measures involving exploration speed (fast vs. slow). It is generally considered that high scores correspond to fast exploration and low scores correspond to slow exploration (Dingemanse et al., 2002; Drent et al., 2003). However, we observed that upon exiting their home cage, birds flew around the room before landing on a tree and, while some remained there (yielding low levels of exploration), others continued to explore the room further (yielding high levels of exploration) (F. Lermite, personal observation). This observation would suggest that low exploration mynas were in fact individuals that sampled their environment quickly, making them fast explorers. This would turn our key finding around by suggesting that more exploratory birds were faster problem solvers. In support of this interpretation, recent research in mynas assessing the convergent and discriminant validity of spatial exploration has demonstrated that individuals that make more frequent contacts with a problem solving task complete exploration of a novel space more quickly than individuals that made fewer contacts with the problem solving task (Perals et al. in prep.).

In sum, our findings provide ambiguous evidence for the idea that individuals faster to solve novel foraging problems display traits typical of proactive behavioural phenotypes. Assuming that problem solving is at least a correlate of cognition (Griffin and Guez 2016; Morand-Ferron et al., 2015), these results could also provide ambiguous support for the idea that fast cognitive styles are associated with proactive phenotypes. Additional experiments measuring more specific cognitive abilities, such as learning speeds and accuracies, coupled with personality measures, are clearly needed (Guillette et al., 2011). Mynas faster to solve a novel foraging problem were no more competitive around food, were not more inclined to take risks around novelty and were less exploratory. On the other hand, faster solving mynas sampled information about the foraging problem at faster rates and the inverse relation between problem solving and spatial exploration might be due to measuring exploration quantity rather than speed. Our discussion highlights the need for greater consensus on how to measure exploratory behaviour (Carter et al., 2013). We suggest this will provide the greatest advancement to our understanding of relationship between cognition and personality.

Acknowledgments

We thank the staff at the University of Newcastle Central Animal House for caring for the captive myna colony. We thank Marie Diquelou for trapping birds for this project. We extend our thanks to Kim Colyvas for statistical assistance.

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