Original Article

Cognition, personality, and stress in budgerigars, *Melopsittacus undulatus*

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To study the fitness effects of individual variation in cognitive traits, it is paramount to understand whether traits such as personality and physiological stress influence cognitive performance. We first tested whether budgerigars showed both consistent personalities and cognitive performance across time and tasks. We tested object and food neophobia, and exploratory behavior. We measured cognitive performance in habituation, ability to solve foraging problems, spatial memory, and seed discrimination tasks. Budgerigars showed consistency in their neophobic tendencies and these tendencies were associated with their exploratory behavior. Birds were also consistent in how they performed in most of the cognitive tasks (temporal consistency), but were not consistent in their performance across tasks (context consistency). Neither corticosterone levels (baseline and stress-induced) showed a significant relationship with either cognitive or personality measures. Neophobic and exploratory tendencies determined the willingness of birds to engage only in the seed discrimination task. Such tendencies also had a significant effect on problem-solving ability. Our results suggest that consistent individual differences in cognitive performance along with consistent differences in personality could determine response to environmental change and therefore have important fitness consequences.

Key words: **Budgerigar, cognition, cognitive performance, neophobia, personality, stress.**

INTRODUCTION

Cognition encompasses all the neural mechanisms through which animals perceive stimuli, process and retain information, and make decisions (Shettleworth 2001). Social behavior, individual recognition, mate selection, parental care, dispersal, foraging, and predator avoidance are all examples of behaviors in an individual's life cycle that require the use of cognitive skills (Shettleworth 2010; Morand-Ferron et al. 2016; Cauchoix and Chaine 2016). Despite the impacts of cognitive skills on an individual's fitness, the action of natural and sexual selection on cognitive traits remains poorly understood (Morand-Ferron et al. 2016). In order to study how evolutionary mechanisms shape cognitive traits, it is necessary to assess the extent and impact of individual variation in cognitive traits (Thornton and Lukas 2012; Sauce and Matzel 2013; Morand-Ferron et al. 2016) and studies have demonstrated substantial individual variation in cognitive traits (Healy et al. 2009; Thornton and Lukas 2012; Buchanan et al. 2013; Thornton et al. 2014). Measuring cognitive traits is particularly challenging because they cannot be measured directly by observation, but rather through behavioral manifestations resulting from cognitive processes, therefore it is critical to determine the effects of potential confounds that are not the result of underlying cognition (Thornton

et al. 2014). To better understand the evolutionary maintenance and fitness effects of variation in cognitive traits, studies must examine the effects and interactions of additional traits that may underlie this variation, such as personality and physiological stress responses (Rowe and Healy 2014; Morand-Ferron et al. 2016).

Animal personality, also termed "behavioral syndromes", has been defined as consistent behavioral differences across contexts and time (Sih et al. 2004). Personality has been of great interest in behavioral ecology for the past decade in wide variety taxa (Bell 2007), partly due to potential fitness consequences of individual personality types (Smith and Blumstein 2008). Personality traits are influenced by hormonal responses, particularly by hormonal reactivity to stressors (Cockrem 2007; Carere et al. 2010; Koolhaas et al. 2010). In general, it is thought that individuals can be categorized as having either proactive or reactive personalities. Proactive personalities in birds generally present as individuals who are more aggressive, bolder, faster explorers, less behaviorally flexible, less sensitive to environmental changes, and who have lower stress responses. In contrast, reactive individuals tend to be less aggressive, shyer, slower explorers, more flexible, more sensitive to environmental stimuli, with high physiological responses to stress (Cockrem 2007; Carere et al. 2010; Cockrem 2013).

Animal personality, as a source of individual variation in behavior, has the potential to account for variation in cognitive styles, which refer to the way in which animals acquire process

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information, and act upon it. For instance, individuals with different personality types might consistently differ in the speed at which they sample their environment (Carere and Locurto 2011; Sih and Del Giudice 2012). Several studies have shown a link between personality and cognitive performance (reviewed in Carere and Locurto 2011; Griffin et al. 2015). One way in which personality might influence cognitive performance is that individuals who consistently tend to be more exploratory and bolder are more likely to encounter novel problems and be more willing or able to attempt solutions to these problems (Reader and Laland 2003). For example, Carib grackles, *Quiscalus lugubris*, that exhibited innovative foraging behaviors, showed higher exploration and lower object neophobia (Overington et al. 2011). Amy et al. (2012) found that great tits (*Parus major*) from a line selected for slow exploration, took more trials to reach the learning criterion in a color association task than birds selected to be fast explorers. European starlings, *Sturnus vulgaris*, that took less time to feed in a new environment, also took less time to solve a foraging task (Boogert et al. 2006). In juvenile Chimango caracaras, *Milvago chimango*, lower neophobia levels were associated with higher problem-solving performance (Biondi et al. 2010). Slow exploring black-capped chickadees (*Poecile atricapillus*) show higher performance in a learning task than fast-exploring chickadees (Guillette et al. 2015). All of these studies suggest that personality type influences performance in certain cognitive tasks. However, these studies have been limited to linking personality traits to only 1 or 2 cognitive tasks at a time. It is still unknown whether different aspects of personality have differential effects on performance in different cognitive tasks (Griffin et al. 2015; Thornton and Wilson 2015). Both personality and cognition are multidimensional in nature, and multiple aspects of each must be evaluated in order to better understand their interactions (Thornton et al. 2014; Griffin et al. 2015). Potential context and temporal consistency in cognitive performance in synergy with personality could greatly impact the way animals respond to changes in their environment (Thornton et al. 2014; Griffin et al. 2015). Therefore, in order to understand the link between personality and cognition, it is critical to evaluate both temporal consistency (i.e., within task) and context consistency (i.e., across tasks) in cognitive performance.

Personality is not the only factor that could affect an individual's cognitive performance. Physiological status, in particular the stress response, has a great potential to affect how individuals respond to cognitively challenging situations. For instance, adult mountain chickadees (*Poecile gambeli*) with experimentally elevated corticosterone levels show enhanced spatial memory abilities compared to control birds (Pravosudov 2003). However, house sparrows (*Passer domesticus*) that showed higher learning efficiency in a problem-solving task also had lower integrated corticosterone levels over an extended period of time (Bókony et al. 2014). Recent studies provide increasing evidence that adrenocortical responses to stressors affect cognitive performance (Ruiz-Gomez et al. 2011; Bebus et al. 2016; Jones et al. 2016).

Among birds, parrots are known for their exceptional cognitive abilities (Pepperberg 1994; Hile et al. 2000; Pepperberg 2002; Dooling et al. 2006; Huber and Gajdon 2006; Manabe et al. 2008; Pepperberg 2009; Scarl and Bradbury 2009; Miyata et al. 2011; Tu et al. 2011; Auersperg et al. 2013; Gajdon et al. 2013). They also maintain complex social interactions (Garnetzke-Stollmann and Franck 1991; Ikkatai et al. 2010; Hobson et al. 2014; Hobson and DeDeo 2015) mediated by learned vocalizations (Wright 1996; Balsby and Bradbury 2009; Berg et al. 2011; Dahlin et al. 2013). These cognitive abilities have been attributed to their relative large brain and telencephalon with its densely-packed neurons (Olkowicz et al. 2016), compared to other nonpasserine birds (Iwaniuk et al. 2005). Budgerigars, *Melopsittacus undulatus*, are small gregarious parrots endemic to Australia that form large nomadic flocks that search for food and water sources (Kavanau 1987). They are increasingly used in studies of vocal learning due to their ability to learn vocalizations as adults (Hile et al. 2000; Plummer and Striedter 2002; Hile et al. 2005; Dahlin et al. 2013; Hara et al. 2015; Whitney et al. 2015), however less is known about their other general cognitive abilities (Heyes 2002; Mottley and Heyes 2003), or their personalities (Callicrate et al. 2011; Duggan et al. 2017).

To establish a link between personality and cognitive performance, we tested whether budgerigars showed consistent personalities and cognitive performances across time and across tasks. If individuals are consistent in the way that they perform in cognitive tasks, then cognitive performance between adjacent time points should be positively correlated. We also predicted that cognitive performance would be positively correlated among different cognitive tasks. This correlation among cognitive tasks is expected since they may require common underlying cognitive processes, such as acquisition of information, learning, and decision making. Second, we evaluated the relationship between multiple personality traits and: 1) whether individuals engaged in cognitive tasks (i.e., responsiveness) and 2) cognitive performance in multiple tasks. We predicted that more exploratory, less neophobic, and more sociable individuals ("extroverts") would be more responsive to cognitive tasks and would exhibit higher cognitive performance across tasks than their less exploratory, more neophobic, and less sociable counterparts ("introverts"). Third, we examine the relationship between adult stress and 1) responsiveness in cognitive tasks and 2) cognitive performance in multiple tasks. We expected that individuals with lower stress responses would show a higher responsiveness in cognitive tasks and higher cognitive performance in multiple tasks than individuals with higher stress responses. Lastly, we tested whether stress response is linked to personality traits in budgerigars. If this is the case, we predicted that levels of exploration and sociability would be negatively associated with the magnitude of the stress response, and that neophobia would be positively correlated with the magnitude of the stress response.

METHODS

We tested our predictions by measuring exploratory behavior, neophobia to objects and food, and sociability levels in male budgerigars. We estimated individual responsiveness in cognitive tasks and cognitive performance in relation to: ability to habituate to objects (the most basic cognitive ability sensu Shettleworth 2010), ability to learn how to solve 2 foraging problems (problem-solving and detour-reaching tasks), spatial memory, and visual discrimination (seed discrimination). We also measured baseline and elevated corticosterone levels induced by a standard handling stressor.

Subjects and housing conditions

The study subjects were 42 domesticated male budgerigars. Birds were purchased from a wholesale breeder (McDonald Bird Farm) at the age of 2–3 months. Upon arrival at the New Mexico State University Animal Care Facility each individual was banded with a metal band with a unique number on the right leg, and a color plastic band on the left leg. Individuals were housed in groups of 9–11 birds in flight cages (79 × 52 cm, and 135 cm high) under a 12:12 light:dark cycle. Room temperature was maintained at 24 ±

2 °C under standard fluorescent lighting. Each group housing cage had multiple wooden perches of different thickness and commercial captive bird toys for enrichment. Parakeet seed mix, cuttlebone, and vitamin water were available ad libitum. All experiments were approved by the Animal Care and Use Committee of the New Mexico State University, Protocol 2013–030.

At the beginning of the test series, each bird was transferred to an individual cage (38 × 27 cm, and 30 cm high) with an enrichment toy, cuttlebone, and water available ad libitum. Birds had visual and auditory access to conspecific. Once in these cages, birds were kept at 90% of their free-feeding weight by only providing limited amount of food for 3 h in the afternoon; this was done to motivate them to consume food during tests in the following morning. Experiments were conducted between 0800 and 1200 h, 5–7 days a week. Both personality and cognitive tests were conducted once a day for each individual. One bird died at 7 months of age, before completing all personality and cognitive tests; otherwise all tests were performed on the same cohort of 42 males. All the personality and cognition tests were conducted in a plexiglass cage (31.5 × 48 cm, and 46 cm high) housed in a closed room (3.4 × 1.7 m) with fluorescent lighting and a surveillance camera system (CCTV Security Pros LLC, Cherry Hill, NJ) that allowed the researchers to video record and observe the activity of the experimental subjects. The test cage was equipped with a single door (21 × 21 cm) used to introduced test subjects into the cage. Each bird was moved from its housing cage to the test cage exclusively for the personality or cognitive tests and was moved back to its housing cage

once the corresponding daily test was concluded. Birds were tested individually (or with another bird; see social habituation below) in random order each day.

Exploration tests

Exploratory behavior was evaluated when individuals were between 3–7 months of age ($N = 42$, Figure 1). For this test, birds were introduced to the empty test cage for 20 min on 2 consecutive days. Exploratory behavior in a novel environment (the plexiglass cage used for testing) was assessed from behavior shown on the first day; exploratory behavior in a familiar environment was assessed from behavior shown on the second day. Both trials were recorded with a video camera positioned 2 m from the front of the test cage, which was marked with lines that divided the floor of the cage into 6 equally-sized regions. Exploratory behavior was assessed as the proportion of regions marked on the cage floor that the bird visited within the test period. Note that this measure can also be interpreted as a measure of levels of general activity (see Perals et al. 2017).

Neophobia tests

After evaluating exploratory behavior, multiple tests were conducted to determine individual response to 3 unfamiliar objects (2 of which were novel experimental devices used later in cognitive tests) and 1 novel food item. Neophobia was measured as the latency in seconds to first peck at the food or the object within a trial period of 20 min ($N = 42$). First, at 3–7 months old, birds were tested for
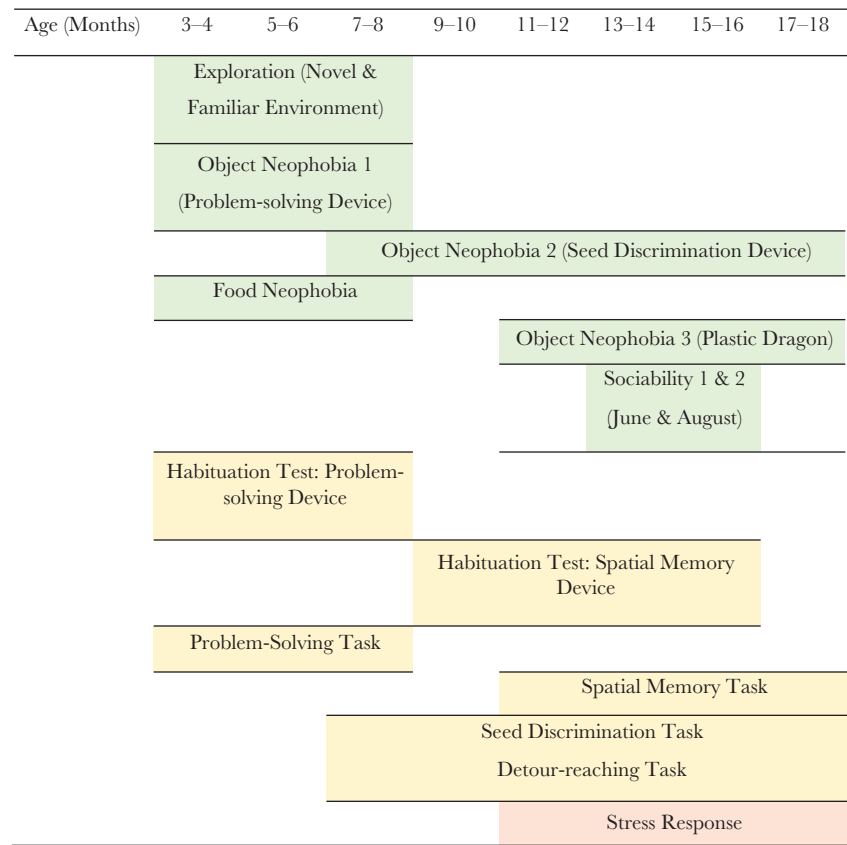

Figure 1
Timeline of personality, cognition, and stress response tests.

object neophobia with the same device that was later employed to test problem-solving ability (Supplementary Figure S1a); here a small yellow plastic cup (also novel to the birds) holding parakeet seed was placed inside of the open problem-solving device. Birds were tested a second time for object neophobia when they were 8–18 months of age by exposing them to the foraging device that would later be used to test seed discrimination. When birds where 11–18 months old, object neophobia was tested a third time using a different novel object (a small plastic statue of a red dragon) next to the food dish used in the housing cages (Supplementary Figure S1d). Food neophobia was tested at age 4–7 months with the first setup described above (Supplementary Figure S1a), but the plastic cup contained a food item completely unfamiliar to the birds before the test (commercial papaya yogurt treats for parakeets).

Sociability

We estimated the ability of our subjects to establish social relationships by quantifying affiliative interactions in single-sex groups. Forty-one males (13–16 months old; Figure 1) were housed in 2 groups of 11, 1 group of 10, and 1 group of 9 individuals in flight cages (79 × 52 cm, and 135 cm high). Groups were formed with randomly selected individuals. A subset of individuals (10–11) from all groups were randomly selected each day for 10 min focal video-recording sessions, preceded by a 5-min acclimation period. The experimenter sat with the video camera approximately 3 m away from the cage where the birds were housed, inside a 3.4 × 3.2 m room. Video-recording sessions were conducted between 1000 and 1600 h, 5–7 days a week. Video-recording sessions were repeated 3 times in order to obtain a total of 30 min of recording for each individual. Social behaviors were sampled in the same manner a second time 2 months later (Figure 1). Data for one of the social groups from the first sampling period was excluded from the analysis because one of the individuals from that group was genetically identified as a female (this bird was removed from that group for the second sampling period). Agonistic interactions among male budgerigars were extremely rare (0.4 interactions in average per individual in 10 min). Affiliative behaviors (allofeeding, allopreening, and courtship displays) were classified from the video recordings using the behavioral descriptions in Brockway (1964a, 1964b) and Abbassi and Burley (2012). The commonly used social network metric, degree centrality (Opsahl et al. 2010), was calculated to estimate the level of sociability of each individual. Degree centrality is the product of the number of individuals that a focal bird is connected to, and the average weight (number of interactions) to these individuals, adjusted by the tuning parameter α. Here, α was set to 0.5 and the values for degree centrality were standardized due to the different number of individuals in each group.

Habituation tests

The goal of the habituation tests was to evaluate individual capacity to habituate to situations, which is one of the most basic cognitive abilities (Shettleworth 2010). Habituation to objects was tested both in individual and social situations. The social habituation tests were conducted first to accelerate the habituation process through social facilitation. By measuring habituation in a social context, we assessed an individual's ability to monitor the actions of a conspecific and modify their behavior based on those actions, a relevant cognitive ability for a gregarious species such as the budgerigar. Abundant yellow millet, a preferred food item of budgerigars, was placed uncovered in the problem-solving device to facilitate use

of the device by individuals and was available for a maximum of 45 min per day (Supplementary Figure S1b). Social habituation tests were conducted at least twice on 2 consecutive days with 2 randomly selected birds (3–7 months old; Figure 1; $N = 42$). In the first 2 tests, birds were allowed to eat from the device for 20 min every day. Social and individual tests were also conducted separately with the device used to test spatial memory when the birds were 10–16 months old ($N = 41$) (Supplementary Figure S2a). In these tests, yellow millet was readily accessible inside all the compartments for 45 min every day. Only the first 2 social habituation tests with both the problem-solving and spatial memory device were included in analyses. Individual habituation tests were performed with the problem-solving device for at least 3 consecutive days, each day for a period of 20 min, when the birds where 3–8 months old ($N = 42$). Habituation tests with the spatial memory device (training phase of the task) were conducted when the birds were 10–16 months old, 45 min every day (Supplementary Figure S2b). As with the social habituation tests, only the first 2 individual habituation tests were included in analyses. Habituation was also measured with the device used to test seed discrimination (Supplementary Figure S3a). These habituation tests were repeated for 10 min each day for 2 consecutive days when the birds were 8–18 months old ($N = 41$). Individual and social habituation were measured as the latency to eat from the device during tests. Additionally, the number of tests that elapsed before a bird ate from the problem-solving device was included as a measure of individual habituation.

Problem-solving task

The goal of this task was to assess individual ability to learn how to solve a foraging problem. This task is also a reflection of another cognitive ability, an individual's behavioral flexibility, since it presents a foraging challenge that budgerigars do not encounter in their natural environment. In this task, male budgerigars (4–8 months old; Figure 1) were tested on their ability to retrieve a food reward from a clear plastic device with 2 compartments divided by a removable barrier (26 × 16 cm, and 2 cm high) (Supplementary Figure S1c and see video in the Supplementary Material). Birds had to push the clear plastic removable barrier between the 2 compartments (Supplementary Figure S1c) to access the reward. Individuals were first habituated to the problem-solving device as described above. Birds were moved to the shaping phase once they consumed food from the device in 3 individual habituation tests (habituation criterion). Birds were allowed a maximum of 8 weeks to reach the habituation criterion. 6 individuals who did not meet this criterion were not tested in this task. Habituation was followed by the shaping phase. Shaping consisted of progressively reducing the degree of access to the reward by gradually sliding closed the divider of the problem-solving device. Each bird received a total of 20, 5-min shaping sessions over 2–4 days. In order to motivate the bird to eat from the device during the shaping phase, a small piece of millet was placed in the uncovered compartment of the problem-solving device and multiple pieces of millet were placed in the partially covered compartment. Birds were allowed to obtain the food reward from the device for 5 min in the first shaping trial. After 5 min, only the small piece of millet in the open compartment was removed and the second trial started. Once the shaping phase was completed, birds were tested at 3 difficulty levels of the problem-solving task (Supplementary Figure S1c); the most difficult level being when the plastic divider was completely closed and the easiest level when the divider was half-way closed. Each individual experienced a total of 20 shaping trials (maximum duration of each trial was 5 min). Individuals were tested in 3 blocks of 8 consecutive 5-min trials, each

block at a different difficulty level over 3 days. The first trial of the daily sessions was preceded by a maximum of 3 min of free access to millet with the divider of the problem-solving device open. Free access to reward was terminated before 3 min if the bird ate from the device, in which case it was allowed to eat for 10 s. Access to reward was limited by closing the opening of the covered compartment 50%, 75%, and 100%. All birds were tested from the lowest to the highest difficulty level. Performance was measured as the number of trials in which the bird obtained the reward successfully or attempted to obtain the reward, weighted by the difficulty level of the trial. The number of trials in which an attempt was made was also weighted by an arbitrarily chosen factor of 0.25 to account for the effort of trying to solve the task in the problem-solving score. Then problem-solving score was calculated as:

Problem-solving performance = Σ (# successful trials × diff. level) + 0.25 × (# trials with attempts × diff. level)

Spatial memory task

We tested the spatial cognition abilities of males at 11–18 months old using a spatial memory task (Figure 1). The spatial memory device consisted of clear plastic box (10 × 5 cm, and 5 cm high) with 16 equally-sized compartments arranged around 3 larger central compartments. Colored plastic dice were fixed to the center of the device to serve as landmarks (Supplementary Figure S2). Birds aged 11–17 months were habituated socially to the spatial memory device until they consumed food for 2 days (habituation criterion). Birds were allowed to reach the habituation criterion over a maximum of 14 trials. Birds that did not eat from the device during the first 5 trials did not pass to the training phase (N = 11). Procedures to test spatial memory were similar to the ones employed by Farrell et al. (2011). After the habituation phase, the 30 individuals that met the social habituation criterion were trained for a maximum of 8 trials of 45 min each. One small piece of millet was placed in each of 4 randomly selected uncovered compartments (Supplementary Figure S2b). Each bird was trained and tested individually with a different random selection of rewarded compartments. During a testing trial (initially lasting 45 min), if the bird ate all the rewards within 10 min, the trial duration was reduced to 20 min. The compartment numbers that the bird visited and the number of visits to each compartment were recorded after watching the video corresponding to each trial. Individuals that ate the reward from all 4 compartments within 10 min of 2 consecutive trials were moved to the testing phase the following day.

Each male was tested in one 45 min trial every day for 5 days. Four small pieces of millet were hidden in the same 4 compartments that were rewarded during training. The cardboard lid of all compartments was partially closed (Supplementary Figure S2c) such that the birds could easily remove the lid from the rewarded compartments and obtain the reward, but not see the reward, which was hidden in a corner of the compartment (see video in the Supplementary Material). During the first trial only, birds had free access to the 4 rewarded compartments (i.e., uncovered) for 10 min after the 45 min trial. The purpose of this free-access period was to reinforce the reward locations learned during training. Performance in the spatial memory task was measured as the average number of errors that birds made over the 5 trials. A bird was considered to make an error if it visited a compartment that did not have millet, if it inspected an unrewarded compartment, or if it revisited a compartment already searched or in which the reward was already discovered. Out of the 30 males tested in this task, 3 were unresponsive during testing (i.e., they did not visit any of the compartments).

Seed discrimination task

The purpose of this task was to test budgerigars' visual discrimination between edible seed and nonedible husks, a critical cognitive skill that budgerigars require for ground foraging. It was modified from the pebble-seed discrimination task used by Magat and Brown (2009) and required the birds to peck at 50 whole seeds scattered on a background of varied seed husks (different color, size, and shape) that were adhered to a petri dish (Supplementary Figure S3a). The seeds placed in the petri dish in each test were all of the same color, size, and shape. All birds (8–18 months old; Figure 1) were allowed to peck at the seeds for 5 min each day. A test was terminated if the bird did not peck the contents of the petri dish within 10 min. Testing for visual discrimination was not continued if a bird did not peck at the seeds in the first 3 tests. Nineteen birds failed to meet this criterion. Responsive birds were tested 5 times (N = 22). Discrimination performance was calculated as the number of seeds consumed divided by the total number of pecks in each test and then multiplied by 100 to obtain a discrimination efficiency percentage. Overall performance in this task was measured by the maximum discrimination efficiency achieved by the bird over all the trials completed. Discrimination learning was assessed by subtracting the discrimination efficiency in the first test from the highest discrimination efficiency achieved in the subsequent trials. A third measure of performance was quantified as the number of tests elapsed until an individual achieved its highest discrimination efficiency.

Detour-reaching task

This task was employed to estimate the ability of an individual to obtain a food reward when a transparent barrier was placed between the subject and the reward. In this task, we tested an individual's ability to learn that it had to go around the transparent barrier in order to access the food. Ability to solve this task was tested at 8–18 months (Figure 1) with a clear plastic cylinder with 2 openings (9 cm in length, 6.5 cm diameter) (Supplementary Figure S3b and see video in the Supplementary Material). The procedure followed was similar to the one by Boogert et al. (2011). In order to train the birds to obtain food from the openings of a cylinder, an opaque cylinder of the same dimension of the clear cylinder used later for testing (Supplementary Figure S3b) was placed in the housing cage of each individual without any food inside for approximately 24 h. The following day, birds were trained in their housing cages by placing a piece of millet inside the cylinder. The cylinder was checked every day and food replaced if the bird ate the millet. This phase was concluded when the bird ate from the cylinder 3 times. One bird did not meet this criterion. Birds were tested with the clear cylinder in 10 trials that lasted a maximum of 5 min each. The cylinder was rotated 90° after each trial to avoid side biases. A trial was considered successful if the bird extracted the millet from the cylinder. Performance in this task was measured as the percent of successful trials for each individual (detour-reaching score). The number of trials that elapsed until the bird reached the detour was also included as a measure of performance. Detour reaching score was not quantified for 18 individuals that did not peck or eat from the device during testing.

Baseline and stress-induced corticosterone levels

Stress responses were measured when males where 11–17 months old (Figure 1). Blood samples were collected between 8:00 am and 8:30 am, once all the personality and cognition tests were concluded for each individual. We collected approximately 80–200 μL

of blood from the brachial vein. The first blood sample was drawn within 3 min of capture from the individual housing cage to assess baseline corticosterone (Romero and Reed 2005, but see Small et al. 2017). After the initial bleed, birds were held in cloth bags until 30 min after capture, when a second blood sample was collected to measure maximum stress-induced corticosterone (Breuner et al. 1999; Romero and Remage-Healey 2000). Budgerigars exhibit maximum corticosterone levels around 30 min after capture followed by restraint (Supplementary Figure S4). Blood was collected in microhematocrit tubes and held on ice for less than 1 h until plasma was separated from red blood cells by centrifugation at 12,000 rpm for 8 min and stored at −80 °C until analysis.

Plasma corticosterone concentrations were estimated using an enzyme immunoassay (EIA) kit (Arbor Assays, LLC, Ann Arbor, MI, No. K014-H1) following protocols developed for small plasma samples (~10 μL) from northern cardinals (*Cardinalis cardinalis*) (DeVries et al. 2015). The assay was validated for budgerigars using matched samples to one of which a known quantity of corticosterone was added; validation samples were from birds not included in this study. After triple extraction with diethyl ether, extracts were resuspended with assay buffer (400 μL) provided in the EIA kit. All samples from each individual were assigned randomly to a plate and a plate location, and assayed in duplicate on the same plate. Baseline and stress-induced samples for a single individual were on the same plate and not split across plates. Baseline corticosterone levels of 5 individuals were undetected by the assay; therefore, it was not possible to obtain values of stress response for those individuals. Inter- and intra-assay variation was estimated by randomly placing 2 plasma samples from a homogenized plasma pool (northern cardinal plasma) throughout each plate. Inter- and intra-assay variation was 11.6% (N = 3 plates) and 17%, respectively.

Statistical Analyses

Statistical analyses were conducted in R version 3.2.1 (The R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org, accesed 28 August 2017). Social network metrics were calculated with the R package tnet version 3.0.14 (Opsahl 2009). We conducted Spearman rank correlation tests to examine temporal consistency and consistency across tests for both personality and cognitive measures. We did not calculate temporal consistency for the detour-reaching task because 57% of responsive birds completed all the trials in 1 or 2 days. We also evaluated associations between personality measures and as well as corticosterone levels (baseline and stress-induced). We report effect sizes (Spearman's correlations) and confidence intervals at 95%. For multiple comparisons, we consider a relationship between 2 measures to be significant if the range for the correlation coefficient estimate does not overlap with 0.

We performed a principal component analysis (PCA) on a correlation matrix with rotation on personality measures to reduce the number of personality variables that were later used for selected analyses. In order to evaluate whether individual's responsiveness in the cognitive tasks (i.e., whether they engage in the task or not) was personality-dependent, the first 3 principal components, which together explained approximately 70% of the variance, were used to compare unresponsive versus responsive birds on each task. We considered birds to be unresponsive for these analyses if they were tested in the corresponding cognitive task but did not show any response. Only 3 individuals tested in the spatial memory task were unresponsive during testing and therefore this task was not included in the responsiveness analyses. In order to evaluate whether there were personality differences between responsive and unresponsive birds, we fitted generalized linear models with binomial distribution. The 3 principal components from the PCA on personality variables were employed as measures of personality for this analysis. Baseline and stress-induced corticosterone, as well as the age at which the birds were tested in the corresponding cognitive tasks, were also entered in these models.

We employed linear models based on permutation tests with the package lmperm (Wheeler and Torchiano 2016) to evaluate effects of personality, corticosterone levels, and age at testing on cognitive performance in all the tasks. Since these models are fitted with permutation tests, there are no assumptions of a particular distribution of the response variable. We performed a PCA on a correlation matrix with rotation on habitation measures to reduce the number of habituation variables that were used for these linear models. We used the first 3 principal components as response variables in the models. These 3 components explained a total of 63% of the variance (Supplementary Table S3).

RESULTS

Consistency in personality measures

Male budgerigars showed extreme values in both the lower and higher ends of measures of exploratory behavior, neophobia, and sociability. Individuals showed consistent levels of neophobia in the second and third tests for object neophobia (Figure 2). Birds that were more exploratory once they were familiar with the testing cage were also less neophobic in the object neophobia 1 and 2 tests and the novel food test (Figure 2). Individuals showed context consistency in their neophobic tendencies within tests conducted in the same age stage. This consistency is illustrated by the strong positive association between food neophobia and object neophobia 1 (age 3–7 months) and the positive association between object neophobia tests 2 and 3 (8–18 months) (Figure 2). Budgerigars did not show consistent levels of sociability between the first and second sociability measures, which were separated by 2 months (Figure 2).

Temporal consistency in cognitive performance

Eighty-six percent of the individuals habituated to the problem-solving device and were therefore tested in this task. Twenty-four (67%) of the individuals tested for problem-solving engaged in the task, and 12 (33%) were unresponsive (i.e., did not attempt solving the task). From all the individuals that engaged in this task, 58% attempted to solve it, and 42% successfully solved it. Fewer individuals were responsive in the seed discrimination task (54%), and the detour-reaching task (58%). For the spatial memory task, 73% of budgerigars met the habituation criteria and were therefore tested, 89% of these were responsive to the task. Overall, cognitive performance of male budgerigars across tasks was highly variable (Supplementary Table S2).

Budgerigars showed consistency from the first to the second day of social habituation for the problem-solving (Spearman rank correlation: N = 42, R = 0.622, P = 7.4E−13) and the spatial memory devices (Spearman rank correlation: N = 41, R = 0.465, P = 0.002). Males were also consistent from the first to the second day of individual habituation tests for the problem-solving (Spearman rank correlation: N = 41, R = 0.531, P = 3.5E−04), the spatial memory (Spearman rank correlation: N = 40, R = 0.687, P = 9.9E−07), and the seed discrimination devices (Spearman rank correlation: N = 41, R = 0.858, P = 7.4E−13). Birds showed consistency in their daily performance in the problem-solving task as well as in the seed discrimination task (Figure 3). Correlations between day-to-day performances in the spatial memory task were positive, but nonsignificant (Figure 3).
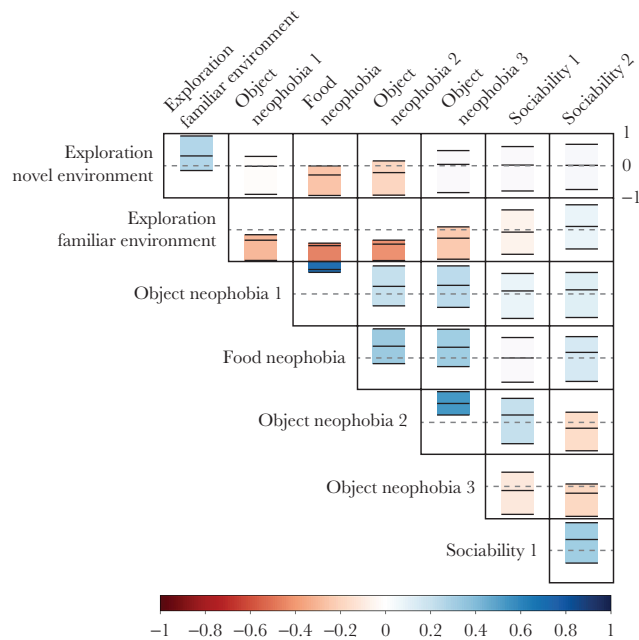
Figure 2
Heat maps indicating strength of Spearman rank correlations (effect sizes) between all measures of personality (arranged by order taken). Blue indicates positive associations and red indicates negative associations. Top and bottom lines of the boxes indicate upper and lower 95% confidence intervals respectively. N for pairwise comparisons was either 41 or 42, except for comparisons including Sociability 1 ($N = 32$).

Associations between cognitive tasks

We found a nonsignificant moderately positive association between the problem-solving task and the detour-reaching task (Figure 4). There were no other associations between performance on other cognitive tasks.

Influences of personality and corticosterone stress response on responsiveness in cognitive tasks

The PCA of personality measures showed that exploration in the novel and familiar environment had the highest positive loadings in the first principal component extracted, whereas problem-solving device and food neophobia loaded strongly in the opposite direction in the same principal component (Table 1). Both measures of sociability showed the highest loadings in the second principal component, and measures of object neophobia 2 and 3 had the highest loadings in the third principal component (Table 1).

Only 3 birds tested for spatial memory were unresponsive in all the trials, therefore this task was not included in these analyses. The first principal component of the PCA on personality variables (exploration and juvenile neophobia) did not have an effect on the level of responsiveness in the problem-solving task and detour-reaching task, however this effect was significant in the seed discrimination task (Table 2). Personality PC2 and PC3 scores, as well as corticosterone levels did not differ between unresponsive and responsive birds in the 3 tasks (Table 2). Age at which the birds were tested in the cognitive tasks did not affect their likelihood of participation in the tasks. These results did not change when we included the 5 individuals with undetectable corticosterone baseline levels (model results not shown).
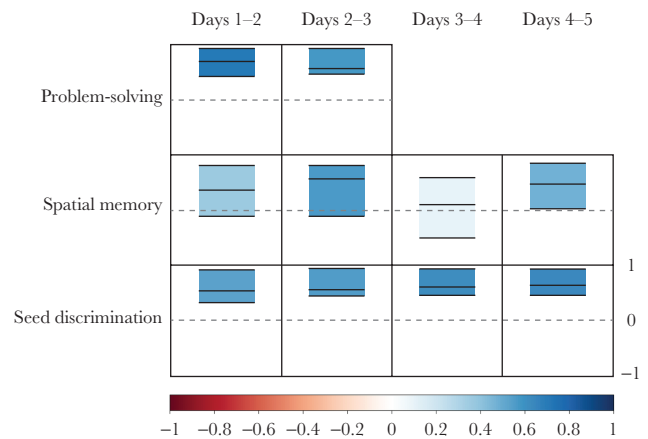
Figure 3
Heat maps indicating strength of Spearman rank correlations (effect sizes) between daily cognitive performance in 3 tasks. The cognitive measures compared here were problem-solving score, maximum seed discrimination efficiency, detour-reaching score, and average number of errors in the spatial memory task. Blue indicates positive associations and red indicates negative associations. Top and bottom lines of the boxes indicate upper and lower 95% confidence intervals respectively. Number of pairwise comparisons: problem-solving task ($N = 36$), seed discrimination task (between $N = 21$ and $N = 23$), spatial memory task (between $N = 9$ and $N = 18$).
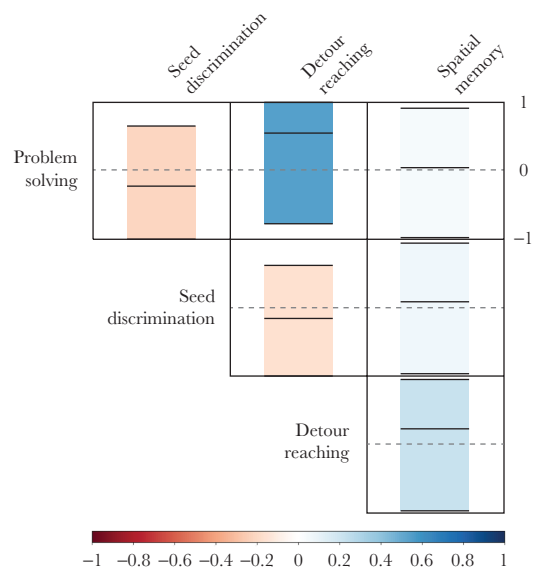
Figure 4
Heat maps indicating strength of Spearman rank correlations (effect sizes) between performance in 3 cognitive tasks. The cognitive measures compared here were problem-solving score, maximum seed discrimination efficiency, detour-reaching score, and average number of errors in the spatial memory task. Blue indicates positive associations and red indicates negative associations. Top and bottom lines of the boxes indicate upper and lower 95% confidence intervals respectively. Number of pairwise comparisons ranged between 17 and 24.

Effects of personality and corticosterone levels, and cognitive performance

We only found a significant effect of exploration and juvenile neophobia (personality PC1) on problem-solving score and ability to habituate to the problem-solving device (habituation PC2) (Table 3). Less neophobic birds habituated faster to the problem-solving

device and also performed better at this task than more neophobic birds. We did not find significant effects of corticosterone levels on cognitive performance in any of the tasks (Table 3). These results did not change when we included the 5 individuals with undetectable corticosterone baseline levels (model results not shown). We only found an effect of age on ability to habituate to the seed discrimination device (Habituation PC1) (Table 3). Birds tested at a younger age habituated faster to the seed discrimination device than birds tested at an older age.

Relationships between personality measures and corticosterone stress response

Most individuals showed increased corticosterone levels after being subjected to a stressor for 30 min, however 3 individuals showed a decrease in corticosterone levels (mean ± standard error. Baseline: 4.01 ± 0.48 ng/ml, $N = 36$; after 30 min: 11.62 ± 0.99 ng/ml, $N = 41$). None of the measures of personality were significantly associated with baseline or stress-induced corticosterone levels (Supplementary Table S1).

DISCUSSION

In order to understand the link between personality and cognition, it is critical to evaluate temporal and context consistency in cognitive performance. We first tested whether budgerigars showed both consistent personalities and cognitive performance across time and tasks. Budgerigars showed consistency in their neophobic tendencies and these tendencies were associated with their exploratory behavior in a familiar environment. Birds were also consistent in how they performed within most of the cognitive tasks (time consistency over consecutive days), but were not consistent in their performance across tasks (context consistency). We investigated the links between personality, corticosterone stress response, and cognitive performance in adult male budgerigars. Exploration and neophobia predicted the ability of birds to habituate to the problem-solving device and their problem-solving performance. Corticosterone levels (baseline and stress-induced) did not show significant relationships with either cognitive or personality measures. Neophobic and exploratory tendencies determined the willingness of birds to engage in the discrimination task. Below we discuss these results and their implications for the evolution of cognition.

Temporal and across-tasks consistency in personality and cognitive performance

Birds were consistent in their neophobia levels toward the problem-solving device (object neophobia 1) and the novel food item presented (Figure 2). However, early measures (juvenile stage) of object neophobia levels did not correlate with later measures (adult stage) performed with different objects (object neophobia 2 and 3). A possible explanation for these results is that budgerigars' neophobia levels change with time, as seems to be the case in Chimango

Table 1

Results of the rotated principal component analysis of the personality tests in male budgerigars ($N = 32$)

	PC1	PC2	PC3
Exploration Novel Environment	**0.228**	−0.122	0.018
Exploration Familiar Environment	**0.477**	−0.064	0.126
Problem-solving Device Neophobia	**−0.472**	−0.043	0.447
Food Neophobia	**−0.491**	−0.01	0.449
Seed Discrimination Device Neophobia	−0.402	−0.15	**−0.554**
Plastic Dragon Neophobia	−0.300	0.230	**−0.395**
Sociability (June)	−0.082	**−0.678**	−0.274
Sociability (August)	0.019	**−0.668**	0.217
Eigenvalue	1.699	1.231	1.084
% Variance explained	36.07	18.94	14.67

The highest factor loading for each variable is indicated in bold.

Table 2

Effects of personality, corticosterone levels, and age of testing on responsiveness in the problem-solving, seed discrimination, and detour-reaching tasks

Response variable	Explanatory variables	Estimate (mean ± SE)	$\mathcal{Z}$ value	P
Responsiveness in problem-solving task	Intercept	−5.524 ± 4.963	−1.113	0.266
	Personality 1	−0.642 ± 0.476	−1.349	0.177
	Personality 2	0.096 ± 0.672	0.143	0.886
	Personality 3	0.804 ± 0.793	1.014	0.311
	Baseline corticosterone	0.284 ± 0.377	0.754	0.451
	Stress-induced corticosterone	0.125 ± 0.093	1.347	0.178
	Age at testing	0.268 ± 0.912	0.294	0.769
Responsiveness in seed discrimination task	Intercept	1.341 ± 2.955	0.454	0.650
	Personality 1	**−1.320 ± 0.478**	**−2.762**	**0.006**
	Personality 2	0.334 ± 0.500	0.667	0.505
	Personality 3	−1.474 ± 0.804	−1.834	0.067
	Baseline corticosterone	−0.049 ± 0.293	−0.168	0.867
	Stress-induced corticosterone	−0.047 ± 0.107	−0.440	0.660
	Age at testing	−0.025 ± 0.195	−0.130	0.896
Responsiveness in detour-reaching task	Intercept	5.258 ± 4.958	1.061	0.289
	Personality 1	−2.069 ± 1.298	−1.594	0.111
	Personality 2	2.795 ± 2.228	1.254	0.210
	Personality 3	−3.345 ± 2.220	−1.507	0.132
	Baseline corticosterone	−0.519 ± 0.463	−1.122	0.262
	Stress-induced corticosterone	−0.343 ± 0.263	−1.304	0.192
	Age at testing	0.046 ± 0.243	0.191	0.848

Age of testing corresponds to the age at which budgerigars were tested in the cognitive task included as the response variable in each model. Personality 1: PC representing exploration and juvenile neophobia. Personality 2: PC representing Sociability. Personality 3: PC representing adult neophobia. Significant results are indicated in bold.

Table 3

Effects of personality, corticosterone levels, and age of testing on performance in each cognitive task

Response variable	Explanatory variables	Estimate	Permutation p-value
Problem-solving score	**Personality 1**	**1.196**	**0.045**
	Personality 2	−1.192	0.190
	Personality 3	1.788	0.070
	Baseline corticosterone	−0.110	0.801
	Stress-induced corticosterone	−0.076	0.544
	Age at testing	−1.830	0.090
Max. seed discrimination efficiency	Personality 1	1.523	0.695
	Personality 2	5.124	0.200
	Personality 3	6.447	0.298
	Baseline corticosterone	1.178	0.457
	Stress-induced corticosterone	−0.591	0.408
	Age at testing	0.574	0.660
Detour-reaching score	Personality 1	−0.008	0.892
	Personality 2	−0.011	0.861
	Personality 3	−0.017	0.887
	Baseline corticosterone	−0.039	0.300
	Stress-induced corticosterone	0.007	0.562
	Age at testing	−0.005	0.855
Average number of errors (spatial memory)	Personality 1	0.328	0.584
	Personality 2	−0.035	1
	Personality 3	1.427	0.226
	Baseline corticosterone	0.481	0.337
	Stress-induced corticosterone	0.129	0.354
	Age at testing	0.613	0.421
Habituation 1	Personality 1	0.125	0.514
	Personality 2	−0.563	0.130
	Personality 3	0.474	0.170
	Baseline corticosterone	0.099	0.513
	Stress-induced corticosterone	0.037	0.416
	Age at testing (problem-solving hab.)	−0.104	0.740
	Age at testing (spatial memory hab.)	0.049	0.851
	Age at testing (seed discrimination hab.)	**−0.322**	**0.034**
Habituation 2	**Personality 1**	**−0.426**	**0.037**
	Personality 2	−0.127	0.653
	Personality 3	0.228	0.485
	Baseline corticosterone	0.127	0.382
	Stress-induced corticosterone	0.005	0.927
	Age at testing	−0.221	0.382
Habituation 3	Personality 1	0.163	0.332
	Personality 2	0.494	0.08
	Personality 3	0.011	1
	Baseline corticosterone	0.0382	0.755
	Stress-induced corticosterone	−0.052	0.210
	Age at testing	−0.184	0.357

Age of testing corresponds to the age at which budgerigars were tested in the cognitive task included as the response variable in each model. Personality 1: PC representing exploration and juvenile neophobia. Personality 2: PC representing Sociability. Personality 3: PC representing adult neophobia. Habituation 1: PC representing by social habituation to the problem-solving device, and individual habituation to the seed discrimination and spatial memory devices. Habituation 2: PC representing individual and social habituation to problem-solving device. Habituation 3: PC represented by social habituation to the spatial memory device. Five thousand iterations were completed in all models until the criterion was met (maximum of iterations was set at 10,000). Significant results are indicated in bold.

caracaras (Biondi et al. 2010; Favati et al. 2015). Alternatively, neophobia levels in budgerigars might not change with age, but birds tend to be intrinsically more neophobic or more neophilic to certain objects than others (Greggor et al. 2015). It is also possible that the neophobia test with the plastic dragon statue (object neophobia 3) may reflect antipredatory responses besides neophobic tendencies in budgerigars. The relationships observed between exploration in the familiar environment and object neophobia 1, the novel food item, and object neophobia 2 suggest that less neophobic individuals, who are more likely to take risks, are also more exploratory or more active in a familiar environment. These relationships are consistent with the body of literature in behavioral syndromes (van Oers and Naguib 2013). Budgerigars were not consistent in their levels of sociability. It is possible that this lack of consistency is

explained by the short observation periods used to sample social behaviors (10 min each observation session for 3 days). These periods might have not been long enough to detect consistent patterns of social interactions among members of the groups sampled. We did not find support for our prediction that exploratory birds would be more sociable. Other studies in different species have found that neophobic individuals tend to be more gregarious (Fogarty et al. 2011; Dardenne et al. 2013). Extensive observations on social behavior in budgerigars are still needed to investigate the relationship between sociability, neophobia, and exploration.

Birds were consistent in their daily performance in the habituation, problem-solving and seed discrimination tasks, but were not significantly consistent in their daily performance in the spatial memory task. This consistency in cognitive performance over time

mirrors temporal consistency found in personality traits. To our knowledge, this is the first study to show temporal consistency in multiple cognitive measures before demonstrating a link between personality and cognitive performance.

Independence between cognitive measures

The lack of strong associations between performance across cognitive tasks in this study might be explained by the fact that these tasks are actually measuring different aspects of budgerigar cognition. Some studies have found positive associations between performance in some cognitive tasks (Bouchard et al. 2007; Isden et al. 2013; MacLean et al. 2014; Anderson et al. 2016). However, other studies have failed to find associations among similar suites of tasks in other species (Keagy et al. 2009; Boogert et al. 2011; Keagy et al. 2011; Isden et al. 2013; Nettle et al. 2015; Shaw et al. 2015). The only positive association, albeit not significant, that we found was between problem-solving and detour-reaching scores. Both of these tasks involve obtaining a reward by either removing or circumventing a barrier, which could explain why birds tended to show similar performance in both tasks. If different tasks are reflecting different aspects of cognition, then consistency in performance across tasks may not be necessary to establish a link between personality and cognition.

Personality determines responsiveness in one cognitive task

Exploratory behavior predicts how likely an individual is to encounter novel situations (Reader and Laland 2003; Reader 2015). This phenomenon would explain why more exploratory and active birds were more likely to engage with the testing device in the discrimination task. These results parallel the results by Overington et al. (2011) that indicate that bolder and more exploratory Carib grackles are more prone to exhibit innovative foraging behaviors. Our results are also consistent with those in European starlings (Boogert et al. 2006) and pheasants (*Phasianus colchicus*; van Horik et al. 2017).

It is surprising that neophobia toward the device itself used for testing (e.g., object neophobia 2) did not determine engagement in the seed discrimination task, but neophobia earlier in life did (i.e., food neophobia and object neophobia 1). It is possible that the petri dish containing seed was not novel enough in order to elicit true neophobic responses in the birds, whereas, the objects employed to test neophobia levels earlier in their life were sufficiently novel enough to elicit this kind of response.

Neophobia and exploratory behavior have limited effects on cognitive performance

We also predicted that neophobia levels and exploratory behavior would be associated with cognitive performance of birds that were responsive in the cognitive tasks. However, neophobia and exploratory behavior only had a significant effect on the ability of birds to habituate to the problem-solving device and problem-solving performance (Table 3). Although these results support the relationship between personality type and cognitive performance (reviewed in Carere and Locurto 2011; Griffin et al. 2015), other studies have not found effects of personality on problem-solving ability (Cole et al. 2011; Zandberg et al. 2017). In direct contrast to our results, Lermite et al. (2017) found that low-exploring common mynas (*Acridotheres tristis*) were actually faster to solve a novel foraging problem. These discrepancies among studies could be due to species-specific relationships between personality and problem-solving

performance, the use of different tasks to assess problem-solving performance, or the use of different estimates of problem solving ability.

The lack of effect of personality and other cognitive measures is consistent with findings from some other studies. For instance, Shaw et al. (2015) did not find any relationship between object neophobia and cognitive measures. Habituation was the most basic cognitive ability tested in our study (Shettleworth 2010), so the habituation tests could be considered the cognitive tasks with the lowest difficulty level that were presented to the birds. A study in great tits found that male exploratory behavior was associated with cognitive performance only in the most difficult stages of an association learning task (Titulaer et al. 2012). However, we found that personality has an effect on both the ability to habituate to the problem-solving (less difficult) device and problem-performance (more difficult). The "cognitive style" hypothesis (Sih and Del Giudice 2012) is based on the idea of tradeoffs between learning accuracy and speed according to an individual's coping style (i.e., proactive vs. reactive). This hypothesis predicts that proactive individuals learn faster, but are less accurate than reactive subjects. Although we did not explicitly test this hypothesis, we found no indication of support for it in our data. For instance, we did not find any correlations between personality traits and either maximum seed discrimination efficiency or how fast budgerigars reached their maximum efficiency. It can be argued that extremely shy individuals were not sampled for learning efficiency and accuracy in this particular task because they did not participate. We could have extended habituation for longer periods of time, however the number of cognitive tasks along with the number of individuals tested imposed limits on the habituation time available for each individual. In our review of the literature, we have found that the majority of studies that measure cognitive performance, in particular those in free-ranging animals, face the issue of only sampling the boldest individuals in the population (e.g., Morand-Ferron et al. 2011; Isden et al. 2013; Shaw et al. 2015; for more examples, see van Horik et al. 2017). However, we found that willingness to participate in a cognitive task was independent of personality type, except for the seed discrimination task. Future studies that seek to test the cognitive style hypothesis could ensure extensive habituation of subjects to testing devices in order to sample those extremely shy individuals, although doing so might reduce the number of cognitive tasks that can be evaluated.

Do corticosterone levels underlie personality and cognitive performance?

We hypothesized that physiological factors, such as corticosterone levels, underlie personality, cognitive responses, and variation in cognitive performance. However, this hypothesis was not supported by our results. We found low and nonsignificant correlations between corticosterone levels and measures of personality and cognition. Furthermore, our results suggest that corticosterone levels do not predict the responsiveness of budgerigars in cognitive tests. We can rule out the possibility of general body condition affecting cognitive performance in the tasks, as all the birds were maintained at approximately 90% of their free-feeding weight during all the tests. Furthermore, since all the birds were food-deprived before testing, variation in motivation to eat should have not played a large role. We are aware that, in practice, it is impossible to completely control the confounding effects of motivation (Rowe and Healy 2014), for instance due to intrinsic individual metabolic differences. Handling stress could have also affected the way individual responded to the

tests, however this effect was likely minimized by our handling of birds daily over extended periods of time. Furthermore, we did not find any effects of stress-induced corticosterone levels on cognitive performance. While we had limited information about the developmental history of the subjects, we think that it is unlikely that early nutritional stress could be causing extreme variation in cognitive performance. These birds were purchased for this study from a single breeder who purposely selected nestlings that showed the best body condition and health (J McDonald, personal communication). The lack of physiological basis for personality in terms of physiological stress that we found here contrasts with findings in other species (Cockrem 2007; Cockrem 2013). It is possible that the history of domestication of the study subjects may have produced this lack of relationship between corticosterone levels and personality traits. We also did not find evidence that supports the existence of a link between stress-induced corticosterone levels in adults and cognitive performance. Further experimental research is needed to demonstrate the possible effects of adult corticosterone levels on cognitive performance.

General discussion

Overall, our results suggest that the effects of personality on the outcomes of tests designed to assess cognitive abilities are more complex than previously described. Neophobic and exploratory tendencies not only may affect performance in tasks designed to test cognitive abilities, but they could also determine whether individuals even participate in these tasks. In order to estimate the whole range of individual variation in cognition, it is critical to avoid sampling bias toward individuals with certain personality types (Morton et al. 2013; Stuber et al. 2013). This potential bias could negatively impact field studies with free-ranging birds that participate voluntarily in tests, as well as laboratory studies with the same scheme, or with strict training criteria, which will result in exclusion of shyer individuals. Therefore, researchers should be aware of and take into account the link between personality and responsiveness to cognitively demanding situations in their study species. Designing tasks to measure cognitive performance that resemble, insofar as possible, situations that animals may potentially encounter in nature could be a way to alleviate sampling bias toward bolder individuals. In order to advance our knowledge on the evolution of variability of cognitive abilities, future research should focus on investigating the effects of personality and physiological stress-coping mechanisms on responsiveness in a variety of cognitive tests in free-ranging animals. Consistent individual differences in cognitive performance, as we document here, in synergy with consistent personality differences could greatly determine the way individuals respond to changes in their environment, which could ultimately impact their fitness.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Medina-García et al. (2017).

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