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8 Associative learning is inversely related to reversal learning and varies with nestling
9 corticosterone exposure

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Associative learning is inversely related to reversal learning in adult Florida scrub-jays and varies with nestling corticosterone exposure

Intraspecies differences are cornerstone to natural selection, yet individual differences in cognition in free-living populations have received little attention. Proactive and reactive coping styles describe individual differences in personality and related stress physiology; however, the coping style model can be extended to include predictions regarding measures of cognition. We compared two measures of personality (neophobia and exploratory behaviour) included in the coping style model to cognitive performance on colour-based associative and reversal learning tests in adult Florida scrub-jays, *Aphelocoma coerulescens*. Also, as exogenous glucocorticoid treatment can affect cognitive performance, we examined whether an individual's naturally occurring physiological phenotype, reflected by corticosterone measures obtained during development and at the time of the learning tests, covaried with learning performance. Performance on associative and reversal learning tests were inversely related. Scrub-jays with low levels of corticosterone as 11 day-old nestlings performed better on an associative learning test as adults, and there was a marginally nonsignificant trend for nestlings with high levels of corticosterone to perform better on a reversal learning test. There was also a marginally nonsignificant trend for neophobic birds to perform better on reversal learning tests. There were no relationships either between adult stress-induced corticosterone levels and learning or exploratory behaviour and learning. Our findings provide evidence that variation in sensitivity to environmental conditions, as reflected by an individual's coping style, underlie the specific strategy by which individuals perform cognitive tasks (i.e., cognitive style). Florida scrub-jays experience a trade-off in performance between types of learning that covary with early corticosterone exposure.

Keywords: behavioural flexibility, cognitive style, coping style, corticosterone, exploratory
behaviour, glucocorticoid, learning, neophobia, personality

In recent years, individual differences within species have received considerable attention (Cockrem & Silverin, 2002; Cole, Cram, & Quinn, 2011; Dingemanse, Both, Drent, & Tinbergen, 2004). Personality, behavioural syndrome, coping style, and temperament are among the terms commonly used to describe consistent, individual differences in behaviour (Gosling, 2001; Koolhaas et al., 1999; Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Sih, Bell, & Johnson, 2004). Additionally, recent studies have shown that individuals commonly display consistency in their performance on cognitive tests (e.g., problem-solving in great tits, *Parus major*: Cole et al., 2011; association and discrimination tasks in black-capped chickadees, *Poecile atricapillus*: Guillette, Hahn, Hoeschele, Przyslupski, & Sturdy, 2015). Shettleworth (1998) defined cognition as, “the mechanisms by which animals acquire, process, store, and act on information from the environment” (p. 5). As such, cognition cannot be directly measured, but psychologists have devised a number of tests to assess certain cognitive abilities, often by assessing learning ability. For example, the Morris water maze is a well-known laboratory test used to assess spatial learning in rodents (Vorhees & Williams, 2006). Modifications of protocols and testing conditions allow for insight into a subject’s cognitive processes. However, in such tests only behaviour can be measured not cognition *per se*. In this way, our understanding of cognition is directly influenced by an individual’s behaviour. It can be argued that cognitive performance is actually a combination of cognitive ability and *cognitive style*. Cognitive ability is an individual’s capability to acquire, process, store, and use information, whereas cognitive

style is the *specific strategy* by which the individual acquires, processes, stores, and uses the information (Carere & Locurto, 2011; Griffin, Guillette, & Healy, 2015; Sih & Del Giudice, 2012).

Influences of Cognitive Style on Cognition

To illustrate, during a test in which an award can be obtained by pushing a red lever, a test subject may have the cognitive ability to discriminate different colours, make the connection between red and the reward, remember this information, and then recall it when presented with a selection of levers. However, the subject's cognitive style (e.g., how the individual focuses its attention) may influence performance on a standardized laboratory test. One individual may continue to push the red lever to obtain a reward while ignoring other stimuli that may also allow the subject to obtain a reward (e.g., different coloured levers), whereas a second individual with the same cognitive abilities may continue to collect information from their environment (e.g., push other levers). Sih and Del Giudice (2012) describe this as a type of cognitive style that is based on a *speed – accuracy* tradeoff. The first subject quickly makes a decision to obtain the reward from pushing the red lever (*speed*), whereas the second individual may be slower at mastering the test, but makes a more complete and *accurate* assessment of the environment. In an associative task, as described above, the first subject will perform better. However, in a reversal learning test, a measure of behavioural flexibility, the second subject will perform better due to more thorough sampling of the environment by trying other levers.

Sih and Del Giudice (2012) propose that the “speed – accuracy trade-off” cognitive style may closely align with individual differences in behaviour, such as those described by proactive and reactive coping styles. Proactive individuals are less sensitive to external stimuli and more “intrinsically driven,” whereas reactive individuals are more sensitive to external stimuli (i.e.,

they are more likely to assess and react to their environment) (Koolhaas, et al., 1999). Consequently, when compared to reactive types, proactive individuals are quicker to approach a novel object, faster to explore a new place, more aggressive towards conspecifics, less flexible in behaviour, and quicker to form routines (Cockrem, 2007; Koolhaas et al., 1999). Additionally in examinations of physiological measures that covary across the proactive – reactive spectrum, proactive individuals generally have lower hypothalamic-pituitary-adrenal (HPA) axis activity as exemplified by a reduced reactivity in response to stressors (Cockrem, 2007; Koolhaas et al., 1999).

“Intrinsically driven” proactive individuals and highly sensitive reactive individuals respond differently to environmental stimuli, which may drive differences in cognitive style, and, subsequently, performance on cognitive tests (Sih & Del Giudice, 2012). Evidence indicates that individuals with proactive traits (e.g., bold, explorative, or aggressive) learn associations better than individuals with reactive traits (guppy, *Poecilia reticulata*: Dugatkin & Alfieri, 2003; cavy, *Cavia aperea*: Guenther, Brust, Dersen, & Trillmich, 2014). Conversely, individuals with reactive traits (e.g., timid, less explorative, or non-aggressive) perform reversal learning tasks better than individuals with proactive traits (black-capped chickadee: Guillette, Reddon, Hoeschele, & Sturdy, 2011; cavy: Guenther et al., 2014). However, the opposite relationship between coping style and learning performance has also been found (great tit: Amy, van Oers, & Naguib, 2012 and Titulaer, van Oers, & Naguib, 2012; black-capped chickadee, Guillette et al., 2015).

Influences of Stress Physiology on Cognition

In addition to cognitive style, stress and glucocorticoids are known to influence cognitive performance, though the nature of the relationship is not always easy to predict (McEwen &

Sapolsky, 1995). Corticosterone is the main glucocorticoid released by HPA axis activation in avian, herptile, and rodent species, whereas cortisol is found in fish and most other mammals (hereafter, both to be termed *CORT*). Elevated CORT affects learning performance across taxa, although the degree to which learning is affected and whether exposure results in benefits or decrements depends on the extent and timing of CORT exposure, as well as the type of learning or cognitive measure in question (de Kloet, Oitzl, & Joëls, 1999; Lupien & McEwen, 1997; Pravosudov, Mendoza, & Clayton, 2003; Roozendaal, 2002). High CORT levels during development may be particularly significant and result in long-term effects on learning (reviewed in Schoech, Rensel, & Heiss, 2011). For instance, chronically elevated CORT levels early in development impair performance on associative and spatial learning tasks later in life (black-legged kittiwakes, *Rissa tridactyla*: Kitaysky, Kitaishkaia, Piatt, & Wingfield, 2003). However, reversal learning may be facilitated by exposure to stress (Japanese quail, *Coturnix japonica*: Calandreau et al., 2011; Norway rat, *Rattus norvegicus*: Thai, Zhang, & Howland, 2013). Similarly, rainbow trout, *Oncorhynchus mykiss*, selected for a high CORT response display greater flexibility in utilizing a new food patch than fish bred for a low CORT response (Ruiz-Gomez, Huntingford, Øverli, Thörnqvist, & Höglund, 2011). To the best of our knowledge, no one has reported a direct relationship between learning and naturally occurring, individual differences in CORT response (i.e., in wild-type individuals that were not artificially selected for a trait).

Present Study

We investigated two factors that may have relationships with cognition: personality and CORT. We tested associative and reversal learning in Florida scrub-jays, *Aphelocoma coerulescens*, as measures of cognition and assessed whether learning performance varied with

two personality traits (neophobia and exploratory behaviour). We also compared learning performance with stress physiology, assessed in nestlings and again just prior to learning tests as birds approached one year of age. While the coping style model includes predictions regarding personality and stress physiology, we did not examine those relationships here, as they were further investigated in a separate study of our population (Bebus, unpubl data).

Based upon descriptions of the proactive-reactive coping styles, we predicted that individuals that: 1) were less neophobic and faster explorers would perform better in associative learning, but worse in reversal learning tests. Additionally, based on links between cognition and CORT, we predicted that individuals that: 2) had low CORT levels during early development would perform better in associative learning tests and poorer in reversal learning tests as adults, and 3) had a low stress-induced CORT response would perform better in associative, but poorer in reversal learning tests.

METHODS

Study System

Florida scrub-jays are cooperative breeders that hold year-round territories (Woolfenden & Fitzpatrick, 1984). The birds live in family groups with a male and a female breeder and up to seven non-breeding “helpers” (Woolfenden & Fitzpatrick, 1984). Helpers aid in territory defense against conspecifics, anti-predator actions (detection, warning, mobbing), and provisioning nestlings and fledglings. They are generally older offspring of the breeding pair that have stayed on their parents’ territory, even though they are reproductively capable by one year of age (Schoech, Mumme, & Wingfield, 1996). Our study population resides in the southern portion of Archbold Biological Station, Highlands County, Florida (27°19’N, 81°21’W, elevation 38-68 m). This population has been monitored for over 25 years, with sex, age, breeding status, and genetic

relatedness known for approximately 200 colour-ringed individuals during any given year (see Rensel, Wilcoxon, & Schoech, 2010; Schoech, Mumme, & Moore, 1991; Small & Schoech, 2015). All protocols were completed under permits issued to SJS from the U.S. Fish and Wildlife Service (TE-117769) and the U.S. Geological Survey Bird Banding Laboratory (23098) and approved by the University of Memphis Institutional Animal Care and Use Committee (0667) and Archbold Biological Station Institutional Animal Care and Use Committee (AUP-006-R).

Neophobia Tests

We categorized individual birds along a continuum of timid to bold based upon their response to a novel object (i.e., individuals that were most timid, or *neophobic*, were more hesitant to approach a novel object). Neophobia tests were conducted in scrub-jays' home territories between 0700 and 1100 hours. Birds had been trained to come to whistles with a peanut reward, and thus were easily attracted to the test site. A small pile of chopped peanuts (approximately 36 g) was placed directly next to or on a novel object. Scrub-jays continue to collect and cache peanuts past satiation, so a bird's current hunger level is less likely to have an effect on their response to peanuts than in a non-caching species. Individuals were identified by unique sequences of coloured and metal leg rings, and tests were carried out in open areas of bare sand to assure that rings were visible. To aid in scoring approach distance, we marked distances of 60 and 30 cm from the center of the novel object using small sticks collected from the surrounding environment. Tests were digitally recorded with a camcorder (JVC HD Everio) on a tripod placed 3 m from the novel object. A researcher stood behind the camera to start the test once birds were observed within the general vicinity. The researcher whistled and tossed a few peanut pieces towards the novel object for 2 min, assuring that the jays were aware of the pile of

peanuts, before quickly leaving the territory. The researcher returned to the territory after approximately 50 min to collect the camcorder and novel object.

Neophobia tests were conducted in Jan. and Feb. of 2012 and 2013 (Fig. 1). In 2012, we used a 60 cm diameter, textured, black rubber mat (with peanuts in the center) and, in 2013, a purple and white striped, plastic ball (approximately 12 cm diameter). We collected the following data from the first 23 min of digital video recordings: latency to first approach within 60 cm and 30 cm, latency to first take a peanut, and total time spent within 30 cm. This time was selected because, at some territories, peanuts were depleted shortly after 23 min. If an individual did not approach within 60 or 30 cm or did not take a peanut, they were assigned the maximum value for that measurement (i.e., 23 min). We tested 139 birds (73 female, 66 male) from 39 territories in 2012, and 127 (66 female, 61 male) from 40 territories in 2013. All birds tested in the population were included in the analysis to determine neophobia scores (see *Statistical Analyses*); however, because learning performance was assessed for a sub-set of non-breeding birds, the neophobia scores of only those individuals were considered in the present study. As neophobia behaviour is repeatable in Florida scrub-jays (Bebus, Jones, Elderbrock, Small, & Schoech, 2015) and other species (Boogert, Reader, & Laland, 2006; Herborn et al., 2010; Verbeek, Drent, & Wiepkema, 1994), a single evaluation of neophobia is likely to be representative of long-term personality.

Although scrub-jays were tested in family groups, social environment does not affect an individual's performance during the neophobia test, as determined by 4 years of repeated testing (Bebus, unpubl data). The number of individuals present (i.e., group size, which ranges from 2 to 9 scrub-jays) during a test does not have an effect on neophobia scores, and scores from an individual are repeatable despite changes in group composition and individual dominance

positions between tests (Bebus, unpubl data). Similarly, a Florida scrub-jay's decision when, or at what distance, to flee an approaching predator (i.e., flight initiation distance (FID)) is not affected by the behaviour (fleeing or foraging) of surrounding conspecifics (Jones, Bebus, & Schoech, 2014). However, Florida scrub-jays may experience social facilitation of learning with repeated, long-term exposure in lower risk environments (Midford, Hailman, & Woolfenden, 2000).

Figure 1. Timeline of tests and blood collection over 2012 and 2013

Captive Tests

We captured non-breeding, helper Florida scrub-jays randomly selected from individuals hatched the previous year (ca. 9-11 months of age; Fig. 1). We collected blood samples (9-45 days after neophobia tests; see *Blood Sampling Methods* for details of capture and blood collection) and transported the birds in individual cloth bags by vehicle to the animal housing facility at Archbold Biological Station. Individuals were held for five days in $1 \times 1.5 \times 1.75$ m cages specifically designed and constructed for this project. We tested birds under captive conditions specifically to eliminate distractions by conspecifics and other factors in the natural environment as previous field-testing attempts failed. Birds were housed in a dedicated room with temperature and photoperiod controlled (25° C and 13L:11D, standard fluorescent light bulbs), with no more than three birds held captive at a time and only one bird in each visually isolated cage.

Individuals received *ad libitum* food (mealworms, waxworms, peanuts, Roudybush maintenance diet, Eukanuba kitten dry food) from the test tray during the initial two days of captivity (see below for description of tray). Water was available *ad libitum* at all times. While two days is a relatively short acclimation time, it was held constant across subjects. We did not want to separate individuals from their family groups longer than necessary and disrupt group social dynamics, and we were restricted by permit specifications, as Florida scrub-jays are federally listed as a threatened species. Birds were returned to their home territories after five days in captivity and all individuals readily reintegrated into their family groups. Initially, 27 (14 female, 13 male) birds from 15 different territories were brought into captivity; however, one male did not readily eat and was returned to his home territory and released on the day of capture.

Learning tests began on the third day of captivity. All tests were recorded digitally (JVC Everio HD Camcorders). A colour-based associative learning task, which we will refer to as the initial learning task, was followed by a reversal learning task. The test tray was made from 70 × 80 cm fiberboard with eight sand-filled wells. It slid in and out of the bottom of the cage between trials and an opaque curtain across the front of the cage allowed the researcher to access trays with minimal disturbance to subjects.

Although food deprivation is commonly used to motivate individuals to perform in the laboratory, we did not withhold food prior to learning tests. However, mealworms, which scrub-jays are highly motivated to obtain, were provided as the reward during the trials. Our group has used mealworms and waxworms in the field for years to both deliver exogenous hormones (e.g., CORT-injected worms; see Schoech et al., 2007) and to census fledglings, as adults will deliver them to the difficult to locate young. In both instances, it is necessary to assure that the

individual to receive a worm is somewhat isolated from other group members as their apparent motivation and desire for these treats leads to competition or jostling to obtain the worm.

As an indirect assessment of whether differences in motivation to obtain the mealworm reward influenced test performance, we measured latency to approach and eat mealworms after the final trial of the day on the fourth day of captivity. There was no indication that motivation influenced learning performance (see *Supplementary Materials*).

Initial Associative Learning

Associative learning is defined as acquiring knowledge of a predictive or causal relationship (association) between two stimuli, responses, or events (Griffin et al., 2015; Shettleworth, 1998). We assessed individual variation in performance on an associative learning test, where the scrub-jays learned an association between a colour cue and a food reward.

Coloured plastic rings were placed around each well on the test tray to create colour cues for the subjects to identify the well with the mealworm reward (2012: two each of blue, green, pink, and orange; 2013: one each of blue and green, three each of pink and orange). We designated blue and green as reward colours and randomly assigned one or the other to an individual for the associative trials. During the first stage of training, two live mealworms were put on top of the sand-filled wells for eight trials. Next, the mealworms were partially buried for eight training trials. For two additional training trials and all of the test trials, thawed, previously flash-frozen mealworms (as live mealworms will move and reveal themselves) were hidden under the sand in the reward wells. Scrub-jays readily take and eat thawed mealworms. Training trials continued, if necessary, until the individual began digging into the sand well to reach a mealworm. At the start of each trial, the test tray was put into the cage with mealworms in place. A trial ended after the bird had inspected at least one well on the tray and returned to a perch. If

the bird did not come to the tray within 12 min, the trial was repeated (i.e., the tray was removed for approximately 5-10 sec then returned to the cage). As a caching species in scrub habitat, Florida scrub-jays often dig in sand to retrieve cached items (Woolfenden & Fitzpatrick, 1984).

In test trials, the coloured rings were moved after each trial, in the same order and pattern for each individual. The sand in every well was leveled and smoothed between trials. Two “probe” trials (i.e., trials in which no mealworms were buried in any well) run at the end of each day were used as *controls*. During the probe trials, subjects continued to dig in wells based on reward colour, which verified that the birds did not use olfactory or visual cues (aside from the coloured rings) to find the reward. In 2012, 14 trials were run and the number of inspections at empty wells (“mistakes”) before probing the reward well was used as a measure of learning. In 2013, test trials continued until individuals reached a threshold of at least 7 correct trials in the last 10 trials (with a minimum of 14 trials total). The difference in protocol between years was to accommodate serial reversal learning trials in 2013 (see *Serial Reversal Learning* below). Subjects from each year were ranked separately, based on performance, due to the difference in learning criteria and test methodology between years.

First Reversal Learning

In reversal learning tests, reward contingencies change so that subjects are required to learn a new association, as well as inhibit a previously rewarded behaviour. In our study, at completion of the initial associative test, reward colours were switched to assess reversal learning proficiency (i.e., if blue had been the initial reward colour, green was now rewarded and vice versa). There was an additional training period of four trials in which mealworms were put on top of the sand in a well of the new reward colour. In 2012, training was followed by 14 test trials. Again, we used the number of inspections at empty wells (“mistakes”) before a subject

located the reward well as a measure of learning. During 2013, trials were repeated until an individual reached at least 7 correct trials of the last 10 trials (with a minimum of 10 trials). Subjects were ranked by performance on first reversal tests separately for each year.

Serial Reversal Learning

In serial reversal learning tests the rewarded cue switches repeatedly. Over successive reversals, successful individuals adopt a “win-stay-lose-shift” strategy and require fewer trials to reach a learning criterion (Shettleworth, 1998). We included serial reversal testing in 2013 to evaluate individual variation in the adoption of a new learning strategy based on experience. For serial reversal trials, the reward colour was switched back and forth between blue and green. The reward colour was changed after a subject completed at least 7 correct trials of the last 10 trials (with a minimum of 10 trials). Birds were assessed based on the average number of trials, over six reversals, that were required to reach criterion. Birds were ranked based on performance, and this ranking was used to compare serial reversal learning performance to initial and first reversal learning performance.

Exploratory Behaviour

An exploratory behaviour test, adapted from the open field tests commonly utilized for laboratory studies on rodents, measured an individual’s response to a novel environment (Verbeek et al., 1994). In 2013 only, following learning tests, birds ($N = 15$) were individually introduced to a test chamber (Fig. 1). Subjects were deprived of food for 30 min prior to the test to help standardize their motivation, as unlike in the learning trials, the exploratory tests were not run concurrently (i.e., we only used one test chamber, so birds were tested at different times throughout the day). The chamber (approximately $1.8 \times 1.8 \times 2.0$ m) was made from 2.5×5 cm lumber with fabric walls and contained: five perches at different heights, three 25×25 cm trays

317 containing sand, a 60 cm (length) log, a water dish (same as in home cage), two palmetto fronds,
318 and eight pine cones. We considered all the objects in the exploratory chamber to be non-novel
319 as they were either present in the cages or are commonly found in scrub-jay habitat. Behaviour
320 was recorded with two video cameras (JVC Everio HD Camcorders) for 150 min. We measured
321 latency to visit each of the 10 familiar objects (5 perches, 3 trays, log, water dish) plus land on
322 the ground. Any object not visited within the 150 min trial was assigned the maximum value
323 (i.e., 150 min). For each individual, we summed the latencies for each of the 11 destinations, and
324 then divided by 11 to calculate an exploratory behaviour score.

325 *Blood Sampling Methods*

326 Birds were bled by venipuncture of the brachial vein with a 27 or 26 gauge needle, and blood
327 was collected in microhematocrit capillary tubes. Blood samples for baseline CORT levels were
328 collected within 3 min of nest disturbance (nestlings) or capture (adults) (Romero & Reed,
329 2005). None of the birds suffered infection or other injury resulting from blood collection.
330 Samples were kept on ice in the field, then centrifuged to separate plasma from the cellular
331 fraction within 3 h of collection, upon return to the lab. Plasma was drawn off and stored at -20°
332 C until analysis.

333 Nestling blood samples were collected on day 11 post-hatch, between 1000 and 1300 h to
334 control for diel fluctuations in CORT levels (Fig. 1). All nestlings in a given nest were removed
335 simultaneously and each was bled by one of multiple researchers within 3 min of nest
336 disturbance. Only baseline CORT was assessed in nestlings to minimize the volume of blood
337 taken (< 140 µl, well within established limits for nestling body weight, McGuill & Rowan,
338 1989). Each nestling was weighed, given one coloured and one metal leg ring, and returned to
339 their nest. We have determined through nest monitoring that scrub-jays readily accept nestlings

back into the nest after our handling and blood sampling protocols (Schoech, unpubl data). The red blood cell fraction of each nestling blood sample was mixed with lysis buffer for genetic sexing.

We captured adult scrub-jays in continually monitored, peanut-baited Potter traps (Fig. 1). A blood sample was collected for baseline CORT within 3 min of capture, with further samples collected at 5, 15, and 30 min post-capture to assess stress-induced CORT levels (Rensel et al., 2010). Between 60 and 140 μ l of blood were taken at each time point. Birds were held in loosely woven cloth bags in the shade between samples. All sampling was completed between 0730 and 1100 h to control for diel fluctuations in CORT levels. After blood samples were collected, individuals were brought into captivity. In 2012, additional blood samples were collected for baseline and a single stress-induced (15 min after removal from cage) CORT level at the end of the captive trials, prior to being returned to home territories (See *Supplementary Materials* for further information).

Hormone Assay

Nestling blood samples collected in 2012 were analyzed using radioimmunoassay (RIA), as in Schoech et al. (1991) and Rensel et al. (2010). All other samples were analyzed with corticosterone enzyme immunoassay (EIA) kits (Cayman Chemical, cat.no.500655) with baseline dilutions at 1:20 and stress series (5, 15, and 30 min) dilutions at 1:100. We validated that RIA and EIA produced similar values of plasma CORT concentrations (see Small & Schoech, 2015).

Corrected Integrated CORT

To quantify the amount of CORT released during a standardized 30 min capture and handling period, we used Prism ver. 5.03 (GraphPad Software, Inc., La Jolla, CA) to measure the area

under the curve of the stress-induced CORT response (i.e., the total CORT exposure). We analyzed this value both with and without correction for baseline CORT levels, which we refer to as “corrected integrated CORT” and “integrated CORT,” respectively (Cockrem & Silverin, 2002; Rensel & Schoech, 2011).

Nestling Experience

Seven of the 28 birds tested had been supplemented indirectly as nestlings through additional food (mealworms) provided to one of their parents by *SmartFeeders* (Bridge & Bonter, 2011). Nestling supplementation history was included in the statistical analysis, but was not significant (see *Statistical Analyses*).

There were only 16 individuals that survived to the following year from the 2012 cohort due to an extremely poor breeding year. For this reason, in 2013 we tested nine birds that, as nestlings, had been handled daily between either day 5 and 11 or 8 and 11 post-hatch as part of an unrelated study. Four of the birds had served as controls and were fed a waxworm injected with peanut oil twice daily, four birds were given waxworms with peanut oil and a carotenoid supplement, and one bird was not fed, but was from a nest in which its siblings were fed waxworms. We excluded nestling baseline CORT values of these nine birds from analysis because they had experienced additional handling prior to the collection of blood samples.

Statistical Analyses

To evaluate an individual’s level of neophobia, we used principle component analysis (PCA) to combine measures (see *Neophobia Tests*) into a single score for each individual. Because none of the behavioural measures had a normal distribution each was log-transformed prior to PCA analysis.

We ranked subjects based on learning criteria to compare an individual's performance in each of the learning tests. We then used Spearman's rank-order correlation with a Bonferroni adjustment of the alpha level ($\alpha = 0.017$) to compare performance pairwise between initial, reversal, and serial reversal learning.

CORT values were standardized to account for year differences in assays (see Small & Schoech, 2015). Corrected integrated CORT and integrated CORT values produced qualitatively similar results, so only corrected integrated CORT results are presented.

For all other analyses, we used separate general linear models. In each model, a learning measure (initial or reversal learning) was included as the dependent variable and a personality (neophobia or exploratory behaviour) or CORT (nestling baseline or adult stress-induced) measure was the independent variable. Sex and nestling supplementation (i.e., *SmartFeeder* or control) were entered as categorical fixed effects and, because health state during development can have long-term effects at multiple levels (Lindström, 1999; Schoech et al., 2011), we included nestlings mass at 11 days of age as a continuous fixed effect. For all analyses, sex, nestling supplementation, and day 11 mass were not statistically significant and were above the arbitrary cut-off P-value ($P > 0.10$), so were not included in the final models. Due to the multiple comparisons, we used a Bonferroni adjusted alpha ($\alpha = 0.0125$) to determine significance. All analyses were run with SPSS 19.0 software (IBM Corp., Armonk, NY).

Dingemanse, Dochtermann, and Wright (2010) proposed that structural equation modeling (SEM) should be used to analyze multiple behavioural measures. However, even the less stringent recommendations advise at least 10 samples for every variable included in this type of model (Kline, 2010). Our sample size precluded the use of SEM, as we had only 26 samples and 6 variables (initial and reversal learning ranks, neophobia and exploratory scores, and

nestling baseline and adult stress-induced CORT levels). Further, we did not have a complete set of measures from every individual in the study, and a multivariate approach would have greatly reduced our sample size. Pairwise comparisons have been used in other studies that examined multiple cognitive measures and additional variables (e.g., Boogert, Anderson, Peters, Searcy, & Nowicki, 2011; Guillette et al., 2015; Keagy, Savard, & Borgia, 2011), and we believe that this is the most appropriate way to analyze our data.

RESULTS

Sample sizes differ throughout the results, as not all individuals completed the learning trials or were present for the neophobia test, and some CORT values were excluded from analysis (see *Nestling Experience*; Table 1).

Figure 2. Initial associative learning and first reversal learning ranks of individual scrub-jays were inversely related. A low score indicates better performance.

Table 1

Sample size for each component

		Total	2012	2013
Training		26	11	15
Learning	Initial	22	10	12
	First Reversal	22	10	12
	Serial Reversal	8	-	8
Personality				
	Neophobia	21	8	13
	Exploratory	15	-	15
CORT				
	Nestling Baseline	16	10	6
	Adult Stress-Induced CORT	25	11	14

Initial and Reversal Learning

Four birds did not complete the initial and first reversal learning trials. Of those four, two did not advance past the training stage, and two completed training, but did not reach learning criteria during the limited captive period.

There was an inverse relationship between initial and first reversal learning rankings ($r_s = -$

0.61, $N = 22$, $P = 0.002$; Fig. 2), a non-significant inverse relationship between initial and serial reversal rankings ($r_s = -0.67$, $N = 8$, $P = 0.069$), and a positive relationship between the first reversal and serial reversal rankings ($r_s = 0.80$, $N = 8$, $P = 0.017$). We did not include serial reversal learning in further analysis because the sample of birds that completed the required sets of trials was low and performance on serial reversal was highly correlated with performance on the first reversal.

Personality and Learning

Figure 3. Neophobic scrub-jays performed worse on initial learning, but better on reversal learning trials than less neophobic birds. A low learning rank indicates better performance. A low neophobia score indicates bold behavior near a novel object. Filled circles, continuous line: initial learning; open circles, dashed line: first reversal learning.

In the PCA to determine neophobia scores, PC1 explained 81.3% of the variance in 2012 and 77.2% in 2013 (see *Supplementary Materials* for more information). There was an inverse relationship between first reversal learning performance and neophobia score; the most timid birds learned the reversal with fewest mistakes ($F_{1,17} = 7.41$, $P = 0.014$, $R^2 = 0.30$; Fig. 3). Though not statistically significant, the least neophobic birds performed better during the initial learning tests ($F_{1,17} = 3.66$, $P = 0.073$, $R^2 = 0.18$; Fig. 3). Exploratory behaviour and initial learning performance were not correlated ($F_{1,10} = 0.21$, $P = 0.66$, $R^2 = 0.020$), nor were exploratory behaviour and first reversal learning ($F_{1,10} = 0.68$, $P = 0.43$, $R^2 = 0.064$).

CORT and Learning

Birds that had lower basal CORT levels as nestlings performed better on the initial learning tests than birds with high nestling CORT levels ($F_{1,11} = 15.11$, $P = 0.003$, $R^2 = 0.58$; Fig. 4).

Conversely, birds with high levels of baseline CORT as nestlings performed better than birds with low baseline levels in the first reversal learning test ($F_{1,11} = 7.01$, $P = 0.023$, $R^2 = 0.39$; Fig. 4).

Circulating CORT levels just prior to testing were analyzed for all but one of the 22

Figure 5. There was no relationship between stress-induced CORT response and initial or first reversal learning. A lower learning rank indicates better performance. Filled circles, continuous line: initial learning; open circles, dashed line: first reversal learning.

Figure 4. Baseline CORT levels measured 11 days post-hatch predicted adult learning performance. A lower learning rank indicates better performance. Filled circles, continuous line: initial learning; open circles, dashed line: first reversal learning.

birds that completed the initial and first reversal trials. One adult baseline CORT value was an outlier (2.7 standard deviations from the mean) and the corresponding stress-induced CORT value was removed from the dataset. Stress-induced CORT levels were not related to initial ($F_{1,19} = 0.60$, $P = 0.45$, $R^2 = 0.030$) or first reversal learning ($F_{1,19} = 0.041$, $P = 0.84$, $R^2 = 0.002$; Fig. 5).

Table 2
Effect size (η^2) and confidence intervals of the regression coefficient

	Initial Learning		Reversal Learning	
	η^2	98.75% Confidence Interval	η^2	98.75% Confidence Interval
Personality				
Neophobia	0.177	[-1.374, 7.342]	0.304	[-6.678, 0.085]
Exploratory	0.020	[-0.009, 0.012]	0.064	[-0.012, 0.007]
Corticosterone				
Nestling Baseline CORT	0.579	[1.234, 9.348]	0.389	[-10.103, 0.598]
Adult Stress-Induced CORT	0.030	[-1.420, 2.526]	0.002	[-1.770, 2.051]

DISCUSSION

Consistent with our initial predictions, we found an inverse relationship between an individual's CORT level as a nestling and performance in an associative learning test as an adult 9 to 11 months later. Similarly, we found support for the prediction of an 'opposite' relationship between developmental CORT exposure and reversal learning performance, although this only approached statistical significance. The predictions generated using the proactive-reactive coping styles garnered some support as more neophobic individuals tended to perform better on the reversal learning task, suggesting increased behavioural flexibility. Additionally, we found a significant negative relationship between associative and reversal learning performance.

The inverse relationship between initial associative and reversal learning performance is predicted by the coping styles model (proactive = routine formation vs. reactive = high

flexibility: Koolhaas et al. 1999, Sih & Del Giudice, 2012). However, few empirical studies have demonstrated this type of relationship (Griffin, Guez, Lermite, & Patience, 2013; Guenther et al., 2014). Studies have more commonly found a positive relationship (Boogert et al., 2011; Guillette et al., 2015) or no relationship (Boogert, Monceau, & Lefebvre, 2010; Guillette et al., 2015) between learning performance on associative or discrimination tests and the corresponding reversal learning tests. When a positive relationship is observed between learning types, some individuals may be overall “better learners” than others. However, Florida scrub-jays appear to experience a trade-off between associative and reversal learning. This trade-off is expected and necessary if sensitivity to environmental stimuli influences cognitive performance, as an individual cannot be both sensitive and insensitive to cues (Sih & Del Giudice, 2012).

Our results show that low endogenous levels of CORT during development were correlated with better initial associative learning and poorer reversal learning performance (though the latter relationship fell short of statistical significance after correction for multiple comparisons). Our finding differs from Crino, Driscoll, Ton, and Breuner (2014) who found that zebra finches, *Taeniopygia guttata*, treated with exogenous CORT early in development learned a novel foraging task more quickly than controls. However, because the effect was observed in only the first of four learning stages, the authors speculated that this likely reflected reduced neophobia in the CORT-treated birds rather than a difference in learning ability.

Developmental CORT exposure can have long-term effects upon numerous behavioural and physiological traits (for review, see Schoech et al., 2011). Our data show a link between low nestling CORT levels and better initial learning, and, possibly between elevated CORT levels and better reversal learning. These observations may be indicative of a physio-behavioural phenotype that includes learning performance and is, at least in part, established during early

development (e.g., by 11 days post-hatch in Florida scrub-jays; Schoech, Rensel, Bridge, Boughton, & Wilcoxon, 2009). Numerous factors may influence both developmental CORT exposure and subsequent learning performance. For instance, nestling diet may affect CORT levels, as food restriction resulted in higher CORT levels in western scrub-jay, *A. californica*, nestlings (Pravosudov & Kitaysky, 2006). However, Pravosudov, Lavenex, and Omanska (2005) did not find a difference in colour-based associative learning with this early nutritional deficit. Curiously, in zebra finches, a high-quality diet early in life was linked to decrements in associative learning performance, although diet quality did not affect reversal learning and CORT levels were not assessed (Brust, Krüger, Naguib, & Krause, 2014; Kriengwatana, Farrell, Aitken, Garcia, & MacDougall-Shackleton, 2015). In our study, however, neither nestling mass nor food supplementation explained the observed variation in associative or first reversal learning.

The mechanism by which CORT during development mediates later cognitive function may involve neuroendocrine organization. In avian species, executive function processes are mediated by the nidopallium caudolaterale (NCL; analog of the prefrontal cortex in mammals; Güntürkün, 2005). This area of the brain has specialized subregions with differential sensitivity to the effects of stress (Holmes & Wellman, 2009). While we cannot establish if CORT had a causal relationship with cognitive performance from our results, we can hypothesize that CORT exposure level during development may have had differential organizational effects on the NCL subregions responsible for facilitating associative and reversal learning (Holmes & Wellman, 2009).

Although not statistically significant, our data suggest that personality and learning performance covary. Sih and Del Giudice (2012) propose that variation in sensitivity to

environmental stimuli may be an important underlying attribute in individuals that explains both personality and cognitive style. Our study did not measure learning speed and cannot explicitly address the speed – accuracy cognitive style described by Sih and Del Giudice (2012). We can, however, consider whether variation in environmental sensitivity underlies personality and cognitive performance. Our data support the prediction that reactive individuals are more sensitive to changes, whereas proactive individuals quickly form and persist in routines regardless of new cues (Benus, Koolhaas, & van Oortmerssen, 1987; Ruiz-Gomez et al., 2011). Anecdotally, many of the scrub-jays that performed poorly on the reversal trials often probed for worms in the previously rewarded colour well and returned to a perch. They did not continue to search, but rather followed a routine that was no longer rewarding. Given that scrub-jays that performed poorly on the reversal trials also tended to be bolder individuals, we may have measured an underlying component of both personality and cognitive style. Less neophobic (proactive coping style) individuals quickly formed routines in the learning trials and did not pay attention to changes in their environment, namely a change in the colour/reward association. Likewise, Bolhuis, Schouten, de Leeuw, Schrama, and Wiegant (2004) and Ruiz-Gomez et al. (2011) reported that, following a similar change in test conditions, unsuccessful individuals appeared to be *stuck* in routines that were no-longer rewarding.

Whilst previous studies reported learning differences between selectively bred lines that differed in stress-induced CORT responsiveness (Amy et al., 2012; Ruiz-Gomez et al., 2011), we did not find a relationship between naturally occurring individual variation in stress-induced CORT response and either measure of learning. We recognize that our relatively small sample size and reduced alpha ($\alpha = 0.0125$ after Bonferroni correction) increase our chance of committing a Type II error (false negative). While our certainty in accepting the null hypothesis

is reduced, we can say with 98.75% confidence that the regression coefficients for our non-significant relationships are unlikely to fall outside of our confidence intervals (Table 2). Conversely, our analysis had a low probability of committing Type I errors (false positive) as a result of the Bonferroni adjustment, which conservatively restricts our α level. Therefore, we can be confident in the statistically significant relationships between initial associative and reversal learning performance and between initial learning performance and nestling baseline CORT.

While motivation to seek a reward, most frequently as a function of hunger, can clearly influence performance in tests such as those used in our study, we consider it unlikely that differences in motivation contributed to the observed variation in cognitive performance. If a difference in motivation were driving the variation in cognitive performance, we would expect that the individuals that did best on the initial learning task would also do best at the reversal task. However, there was a pronounced inverse relationship between performance on the initial and reversal learning tasks (also, see *Supplementary Materials*).

Although speculative, ecological factors are likely to play an important role in the development and persistence of different phenotypes in our study population. As some have proposed, fluctuating environments maintain variation in phenotype, such as personality (Dall, Houston, & McNamara, 2004; Dingemanse et al., 2004). As their name implies, Florida scrub-jays have evolved foraging and reproductive strategies that depend upon scrub habitat that is indigenous to peninsular Florida (Woolfenden & Fitzpatrick, 1984). Due to the dynamic nature of their habitat, Florida scrub-jays may be subjected to the effects of disruptive selection more than most other species (Rueffler, Van Dooren, Leimar, & Abrams, 2006; Wolf, Van Doorn, Leimar, & Weissing, 2007). Florida scrub is naturally maintained by intense wildfires (as frequently as every 5-10 yr), which can quickly and drastically alter the landscape (Woolfenden

& Fitzpatrick, 1996). There may be fitness advantages of a specific coping or cognitive style within a given habitat. For example, individuals may need to exploit new food sources in recently burned areas that have reduced cover and increased predation risk. One can imagine that under such conditions reactive types may fare better, as they are behaviourally more flexible and cautious. Conversely, several years post-fire, individuals with proactive traits may benefit. Ongoing study of differential survivorship across phenotypes in respect to habitat succession will help determine the merit of such ideas in this population.

Developmental experience also influences an individual's phenotype (Groothuis & Carere, 2005; Schoech et al., 2011), which may account for the link between CORT exposure during development and learning in our results. Indeed, early CORT exposure mediated by environmental conditions may prepare or "program" individuals to be better suited for the specific environment in which they are raised (Liu et al., 1997), and cognitive style may be a characteristic that is "programmed" by an individual's environment via CORT exposure.

Conclusion

Florida scrub-jays experience a trade-off in learning performance, as is evidenced by the inverse relationship between performance in initial associative and reversal learning trials. Individual differences in sensitivity to environmental cues may underlie this trade-off. Similarly, our results suggest that phenotype is constrained, as no individuals were among both the most bold and most flexible. There is no "best" phenotype associated with learning, as no individuals were "best" overall learners. Developmental levels of CORT were predictive of learning performance, but at this time we cannot address whether there was a causal effect of CORT on learning. We encourage more studies that explore both the factors that mediate the formation of

an organism's physio-behavioural phenotype, as well as the long-term fitness impacts across complex and dynamic environments of such variable physio-behavioural phenotypes.

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