Corticosterone exposure during development improves performance on a novel foraging task in zebra finches

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Developmental stress affects a range of phenotypic traits in later life-history stages. These long-term effects are thought to provide information to potential mates on individual quality and the ability to cope with adversity (i.e. the developmental stress hypothesis). Developmental stress appears to affect learning broadly, but the direction of effect is not always consistent between studies. This disparity may arise from indirect effects of developmental stress on other physiological or behavioural systems, which can affect outcomes in learning paradigms. Here, we examine the effect of elevated corticosterone (the dominant avian stress hormone) during development on the ability of zebra finches, *Taeniopygia guttata*, to learn a novel foraging task as adults. Additionally, we evaluate treatment effects on metabolism, to determine whether changes in metabolic rate indirectly alter learning results. We found that birds exposed to elevated corticosterone during development solved a foraging task faster than control siblings. This outcome could result from differences, not in learning ability, but in motivation for reward. However, we found no difference between treatment groups in metabolic rate. Hence, our results indicate that developmental stress can increase learning ability, and suggest that the effects of stress will vary based on the type of learning studied.

Stress during development can affect a range of physiological and behavioural systems resulting in outcomes such as reduced growth, impaired immunocompetence and altered neurological function (e.g. Liu et al., 1997; Loiseau, Sorci, Dano, & Chastel, 2008; Müller, Jenni-Eiermann, & Jenni, 2009; Weaver et al., 2004). Phenotypic effects shaped by developmental stress can be sustained across an animal's lifetime and, in this way, may have important effects on fitness across life-history stages (reviewed in: Matthews, 2005; Nesan & Vijayan, 2005; Schoech, Rensel, & Heiss, 2011; Spencer & MacDougall-Shackleton, 2011). For example, songbirds learn their species-specific song early in life (Beecher & Brenowitz, 2005; Brenowitz & Beecher, 2005; Marler, 1970). Developmental stress (e.g. food restriction or elevated glucocorticoid stress hormones) decreases development of the brain regions that control song learning and production (Buchanan, Leitner, Spencer, Goldsmith, & Catchpole, 2004; Nowicki, Searcy, & Peters, 2002). Adults exposed to stress during development sing less complex songs and are, consequently, less preferred by females

(Buchanan, Spencer, Goldsmith, & Catchpole, 2003; Nowicki et al., 200; Spencer, Buchanan, Goldsmith, & Catchpole, 2003; Spencer et al., 2005). In this way, adult song signals an individual's ability to cope with an adverse environment during development and is a reliable signal for mate choice (i.e. the developmental stress hypothesis; Nowicki, Peters, & Podos, 1998; Nowicki et al., 2002; Spencer et al., 2003).

Over the years, substantial evidence from studies in both free-living and captive birds has supported the developmental stress hypothesis (reviewed in Spencer & MacDougall-Shackleton, 2011). Recently, the evaluation of this hypothesis has been expanded to examine how developmental conditions affect learning tasks other than song learning. For example, Bonaparte, Riffle-Yokoi, & Burley (2011) restricted the protein content of food for developing zebra finches, *Taeniopygia guttata*, and found that food-restricted birds had reduced ability to solve an associative-learning task as adults (175 days posthatch). Black-legged kittiwakes, *Rissa tridactyla*, chicks exposed to experimentally elevated levels of corticosterone (CORT; the dominant avian glucocorticoid) had a reduced ability to complete an associative-learning task as juveniles and continued to perform poorly 8 months later as adults (Kitaysky, Kitaiskaia, & Winfield, 2003). Other studies have found a positive effect of

developmental stress on learning. Domesticated chickens, *Gallus gallus domesticus*, subjected to social stress during the first 3 weeks of life performed better at an associative-learning task compared to control birds (Goerlich, Natt, Elfwing, & Macdonald, 2012). Likewise, juvenile Japanese quail, *Coturnix japonica*, exposed to repeated negative stimuli (i.e. stress) displayed enhanced behavioural flexibility in a spatial memory task (Calandreau et al., 2011). In summary, developmental stress has broad effects on learning, but the direction of effect is not consistent between studies.

Developmental stress is known to affect a range of phenotypic traits that could indirectly influence learning and potentially explain variable results between studies. For example, in zebra finches, treatment with CORT during the nestling period increased variability in overnight standard metabolic rate (Spencer & Verhulst, 2008). However, this effect was only observed during the treatment period and not in adulthood (Spencer & Verhulst, 2008). In contrast, Schmidt, MacDougall-Shackleton, and MacDougall-Shackleton (2012) showed that developmental stress in the form of food restriction and elevated CORT permanently increases standard metabolic rate in female song sparrows, *Melospiza melodia*. Birds with greater metabolic demands could be differentially motivated by food reward in learning paradigms and, thus, solve paradigms faster independent of learning ability. Developmental stress can also affect activity level and behaviours such as neophobia, which could confound the results of experiments that measure learning using novel objects. Studies incorporating additional metrics of adult phenotype would be better able to elucidate the relationship between development stress and learning.

We examined the effects of elevated CORT during the nestling period on adult learning in zebra finches. We fed zebra finches CORT during the nestling period and measured learning in adult birds (60 days posthatch) using a foraging paradigm that quantifies the ability of birds to access a hidden seed reward (Boogert, Giraldeau, & Lefebvre, 2008; Grindstaff, Hunsaker, & Cox, 2012). Based on the developmental stress hypothesis, we predicted that zebra finches fed CORT during development would solve the learning task more slowly than control birds. Developmental stress can also affect metabolic rate in birds (e.g. Schmidt et al., 2012; Spencer & Verhulst, 2007). Differences in metabolic rate between CORT-fed and control birds could increase energetic needs, resulting in greater motivation to feed and, hence, locate food. Thus, we also tested whether CORT treatment during development affected metabolic rate, which could help explain variation in performance on food-based learning tests.

METHODS

Study Population

We obtained adult domesticated zebra finches from six pet stores across Montana and Washington, U.S.A. We banded the birds with a unique combination of colour bands to identify individual birds. Breeding finches were housed in a 6.1×7.6 m room where they were allowed to interact freely with all other birds. We housed the birds on a 14:10 h light/dark cycle at $26-27\,°C$ with $20-30\%$ humidity. Birds had access to 12 nestboxes and shredded burlap nesting material. We fed birds commercial finch seed (Silver Song West) and spray millet ad libitum and supplemented their diet daily with hardboiled eggs, spinach and crushed eggshells. Nestboxes were monitored daily for signs of nest building and egg laying.

Starting on hatch day, we marked nestlings with an individual combination of leg markings using a black Sharpie marker. Between 3 and 4 days after hatching, we banded nestlings with a numbered plastic leg band. All nestlings in a nest were then randomly assigned to treatment groups (CORT or control). Nestlings exposed to the CORT treatment were fed oral boluses (25 μl) of CORT (Sigma Aldrich) dissolved in peanut oil twice daily approximately 5 ± 1 h apart. From 12 to 15 days posthatch, nestlings received 0.124 mg/ml of CORT in peanut oil for a total daily dose of 6.2 μg of CORT. Starting 16 days posthatch, the dose was increased to 0.163 mg/ml for a total daily exposure of 8.15 μg of CORT. Control nestlings were fed 25 μl of peanut oil on an identical feeding schedule. Nestlings were exposed to treatments from 12 to 28 days posthatch (methods as per Spencer, Evan, & Monaghan, 2009). At 30 days posthatch, zebra finches exposed to CORT treatment had elevated baseline and stress-induced CORT compared to control siblings (mean baseline: CORT: 2.41; control: 1.06 ng/ml; mean stress-induced: CORT: 8.26; control 4.58 ng/ml; Crino, Driscoll, & Breuner, 2014). However, there were no treatment effects on baseline or stress-induced CORT in zebra finches at 60 or 90 days posthatch (Crino et al., 2014).

We noticed no adverse effects from CORT treatment on the health or behaviour of nestlings. Our methods were approved by the Institutional Animal Care and Use Committee of the University of Montana (protocol number AUP 018-11).

Learning Paradigm

We measured learning ability in zebra finches 60 days posthatch (± 2 days) using a foraging paradigm with four levels of escalating difficulty (methods as per Boogert et al., 2008). We presented birds with a plastic grid ($26 \times 22 \times 2$ cm) containing 10 wells (0.8 cm deep and 1.3 cm wide) covered with lids fitted with rubber bumpers on the bottom (3.5 cm in diameter). For each level, we placed two seeds of millet in every well of the testing apparatus. To proceed to the next level of difficulty in the paradigm, birds had to access and eat the seeds from at least two wells. For the first level of difficulty, we placed the lids next to the holes. For the second level, we placed the lids so they covered half of each well. For the third level, we covered the wells with the lids entirely, and for the fourth level, we pushed the rubber bumpers into the wells. To pass the fourth level of difficulty, birds had to pry the lids off with their beaks to access the seeds. Birds that solved the task in the fewest trials were considered superior learners (Boogert et al., 2008).

We isolated test birds in wire cages ($33 \times 38 \times 43$ cm) 24 h preceding the learning test in a room separate from the main colony. To prevent the birds from seeing each other during the test we placed opaque barriers between the cages. We removed all food from cages 1 h before the lights were turned off in the testing rooms at night, and we began the learning trials 1 h after the lights were turned on for the day. This protocol allowed us to standardize the fasting time and control for potential differences among individuals in motivation to solve the foraging paradigm. Birds were housed on a 14:10 h light/dark cycle and so were food deprived for 10 h at night and 2 h during the day. We observed no adverse effects of food deprivation on the health or behaviour of the birds. Throughout the course of the experiment birds had access to water ad libitum. We started the learning trials at 0730 hours. Learning trials were recorded using Veho Muvi microDV camcorders. An observer started the camera at the beginning of each trial before leaving the testing room. For each learning trial, birds had 15 min to solve the task and pass to the next stage. After each learning trial, we removed the lids from the apparatus to allow the birds access to the seeds in the open wells for 45 min before starting the next trial, to provide adequate nutrition during the experiment. Birds that failed to pass a stage were exposed to the previous stage in the next trial. For example, if a bird failed to pass stage 3, it was presented

with the stage 2 paradigm in the next trial, and it had to pass this stage once again before attempting stage 3 a second time. The learning test spanned 2 days with a total of 17 trials possible to solve the task: nine trials on the first day and eight trials on the second day. We used the cumulative number of trials that birds took to solve the learning test as the measure of learning performance (range 4–17 trials), with a score of 4 indicating that birds passed each stage in one trial. If birds failed to solve the fourth stage of the learning test by the 17th trial, they were assigned a learning score of 18 regardless of the final stage passed (i.e. stages 1–3).

We randomly chose two birds from each nest ($N = 19$ nests) to be used in this study. Therefore, $N = 19$ per treatment group.

Basal Metabolic Rate

We measured basal metabolic rate (BMR) in a separate cohort of birds 60 days posthatch (± 2 days; $N = 9$ for CORT and 13 for control) as oxygen consumption (VO_2) in an open flow system using an oxygen analyzer (Foxbox; Sable Systems, Las Vegas, CA, U.S.A.). On the day of the measurement, food and water were removed from the cage 3 h before the beginning of the metabolic recording to have the sample in post absorptive state. The test was performed starting at 2000 hours to overlap the night cycle of the birds and measure metabolic rate in a resting state. We measured body mass of our samples using an ACCULAB portable electronic scale (ACCULAB, Elk Grove, IL, U.S.A.) with an accuracy of ± 0.001 g. Each bird was put in an airtight 3.2-litre stainless-steel metabolism chamber, where it could perch on an iron mesh. The chamber sat in a large insulated box with a Peltier device (Pelt-4; Sable Systems) to maintain temperature at 30 ± 0.1 °C. This temperature is within the thermoneutral zone of small passerines (Eberhardt, 1994). The chamber was connected to an open-flow system and flushed with atmospheric air scrubbed from CO_2 and water vapour at a rate of 200 ml/min, which ensures a stable proportion of available oxygen for birds weighing 13–16 g. Exiting air was filtered through scrubbers with soda lime, magnesium perchlorate and Drierite to remove water and CO_2. We allowed birds to acclimate to the chamber for 1 h and then measured VO_2 continuously every 0.5 s until a plateau (maximum oxygen consumption) was reached and maintained. The total amount of time needed to complete a measurement ranged from 210 to 320 min. VO_2 (ml/h) was calculated as the O_2 concentration value for the most stable 10 min of oxygen consumption within the plateau using ExpeData software (version 1.3.2, Sable Systems).

Statistical Analyses

The numbers of cumulative trials needed to pass all four learning stages were non-normally distributed (Shapiro–Wilk test: $P < 0.01$ for all). We log transformed the number of cumulative trials and used the resulting values in unpaired analyses. We used a general linear mixed model to analyse treatment effects with the number of trials needed to solve each learning stage as the dependent variable, sex and treatment as fixed factors, nest of origin and individual as random factors, and stage (1–4) as a covariate. We found no effect of sex on learning ($F_{1,57} = 0.24, P = 0.62$) and no sex∗treatment interaction ($F_{1,57} < 0.23, P > 0.63$), and we removed both of these terms from the final model. We compared siblings from different treatment groups using paired t tests for each stage, with the number of trials to solve the stage as the dependent variable. It is possible that the number of trials needed to solve stages 2, 3 and 4 was influenced by the number of trials needed for the birds to initiate feeding on the testing apparatus (stage 1). We examined this by subtracting the number of trials needed to pass stage 1 from the number of trials needed to pass

stages 2, 3 and 4. We then used these resulting values in paired t tests. We also used a general linear mixed model to analyse differences in the rate of learning between treatment groups (i.e. slopes indicating how rapidly birds progressed through learning stages), with the number of trials to pass each stage as a dependent variable, treatment and stage as fixed factors, and nest of origin and individual as random factors. We included sex as a fixed factor in initial models, but it was nonsignificant ($F = 0.02, P = 0.89$) and, hence, was excluded from the model. We used a treatment∗stage interaction to test for differences in rate of learning between treatment groups.

We used linear regression to evaluate average VO_2 consumption against body mass. Basal metabolic rate showed a nonsignificant tendency to increase with body mass ($F_{1,20} = 3.32, P = 0.083, r^2 = 0.38$). Body mass has well-known effects on metabolic rate, and our data support this relationship. For this reason, we used residual VO_2 consumption after accounting for body mass in all analyses of basal metabolic rate. We used univariate analysis of variance (GLM) with sex and treatment as fixed factors to examine the effects of sex on basal metabolic rate. Sex had no effect on basal metabolic rate ($F_{1,20} = 0.18, P = 0.8$), and so was excluded from further analyses. We used ANOVA to examine differences in basal metabolic rate between treatment groups. We calculated effect size for metabolic data as the difference between the means of the two treatment groups divided by the pooled standard deviation (Cohen's d). We considered values above 0.5 to indicate an adequate sample size (Cohen, 1992).

We conducted all statistical analyses using PASW statistical software (version 18).

RESULTS

Learning Paradigm

Zebra finches exposed to CORT during development solved each stage of the learning test in fewer trials than control birds ($F_{1,18} = 11.61, P = 0.003$), and CORT-exposed siblings solved each stage of the novel task in fewer trials than control siblings (paired t test: $t_{18} < -2.61, P < 0.02$ for all stages; Fig. 1). However, once we accounted for differences in the number of trials needed for each sibling pair to pass stage 1 (paired t test: $t = -3.28, P = 0.004$), there were no differences in the number of trials needed to pass each subsequent stage ($t_{18} > -0.19, P > 0.4$). In other words, the differences between the treatment groups in the number of trials needed to pass stages 2, 3 and 4 were driven entirely by the difference in the number of trials needed to pass stage 1 (Fig. 2). In support of this, we found no difference in the rate of learning between the two treatment groups (treatment∗stage effect: $F_{3,108} = 1.13; P = 0.34$).

Basal Metabolic Rate

The average $\pm$ SE basal metabolic rate was 0.88 ± 0.10 ml/h for CORT-treated birds ($N = 9$) and 0.82 ± 0.11 ml/h ($N = 13$) for control birds. CORT treatment during development had no effect on basal metabolic rate (ANOVA: $F_{1,20} = 1.64, P = 0.22, d = 0.57$; Fig. 3).

DISCUSSION

Zebra finches exposed to CORT during development solved a foraging paradigm in fewer trials than control siblings. However, this trend was heavily influenced by the number of trials needed to pass the first stage of the foraging task. Once we accounted for variation in the number of trials needed to pass the first stage, we found no difference between treatment groups in the number of
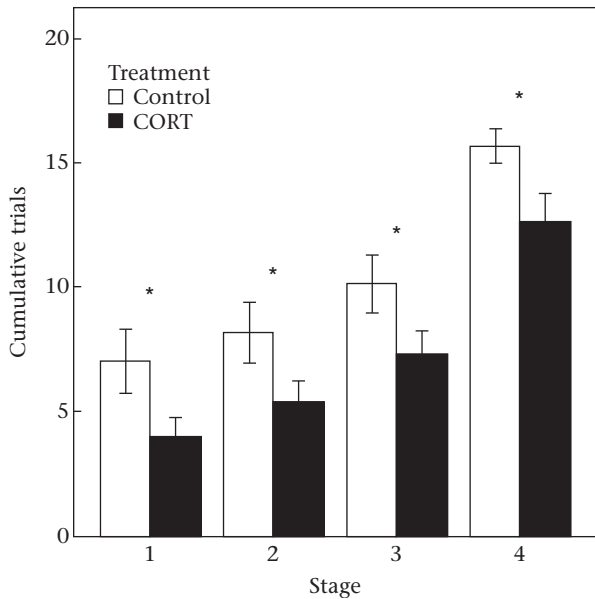
Figure 1. Mean ± SE cumulative number of trials that zebra finches in each treatment took to complete each stage of the learning test. Subjects were either exposed to corticosterone (CORT, $N = 19$) or a control treatment (control, $N = 19$) during development. *$P < 0.02$.

Figure 3. Effects of corticosterone (CORT) treatment during development on basal metabolic rate of zebra finches. Box plots show the 25th and 75th percentiles (boxes), median (line within box) and the 10th and 90th percentiles (whiskers).

trials needed to pass the remaining three stages of the learning task. These results could indicate that once zebra finches located the millet seeds in the testing apparatus they had sufficiently learned to associate the food reward with the apparatus. Therefore, increasing the difficulty of obtaining this reward did not constitute an additional measure of learning ability. In this scenario, zebra finches exposed to CORT during development would be considered better learners compared to control siblings.

Our findings contrast with an overwhelming majority of studies with passerines showing that developmental stress decreases learning (e.g. Buchanan et al., 2003; Nowicki et al., 2002; but see counterexamples in the Introduction). In particular, developmental stress is known to decrease song learning, a trait important for
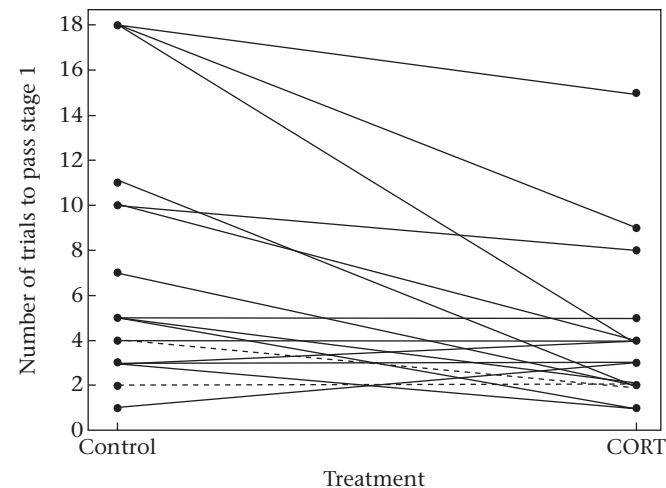

Figure 2. Number of trials required to solve stage 1 of the learning test by sibling pairs of zebra finches that were either exposed to corticosterone (CORT, $N = 19$) or a control treatment (control, $N = 19$) during development. Solid lines indicate $N = 1$ sibling pair; dashed lines indicate $N = 2$ sibling pairs. A larger number of trials indicates slower learning.
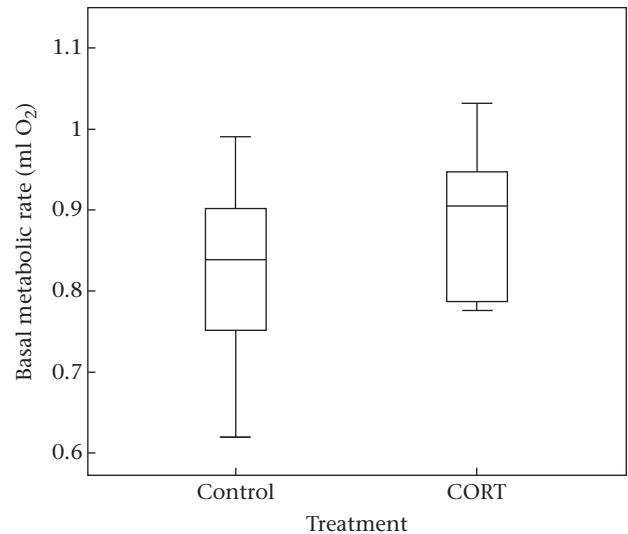
reproductive success. There is increasing support for an adaptive role of developmental stress in shaping animal phenotype to match environmental conditions (phenotypic programming; reviewed in: Henriksen, Rettenbacher, & Groothuis, 2011; Schoech et al., 2011). Developmental stress may create resource trade-offs that cause individuals to invest in some neural structures at the expense of others during development. In this scenario, developmental stress may decrease some types of learning (i.e. song learning) but increase other types (i.e. foraging tasks). Alternatively, incongruous findings between studies could result from variation in the amount of stress (e.g. glucocorticoids) to which test animals are exposed. Glucocorticoids can have dose-dependent effects on learning, where low and high doses have negative effects on learning, and intermediate levels have positive effects (Diamond, Bennett, Fleshner, & Rose, 1992). In our study, we evaluated the effect of one dose of CORT treatment on learning. It is possible that we exposed zebra finches to an 'intermediate' CORT dose during development and, thus, observed an increase in learning ability.

Developmental stress could also cause programmatic effects on learning by permanently changing hypothalamic–pituitary–adrenal (HPA) axis activity, which modulates the release of glucocorticoids (GCs). In some systems, developmental stress increases HPA axis function so that animals exposed to developmental stress have greater GC output as adults (e.g. Hayward & Winfield, 2004; Spencer et al., 2009). In this way, developmental stress could affect adult learning by altering the amount of GCs to which an animal is exposed, which affects learning. In our system, we found that zebra finches fed CORT during development had elevated baseline and stress-induced CORT in response to restraint stress at 30 days posthatch, but not at 60 nor 90 days posthatch (Crino et al., 2014). This suggests that the effects of developmental stress on learning are not being determined via programmatic effects on the HPA axis, but rather on programmatic effects on other systems (see above). However, social isolation can increase CORT output in gregarious birds (Apfelbeck & Raess, 2008). It is possible that testing zebra finches in social isolation from other birds induced a stress response that we did not capture using a restraint stress protocol (e.g. Apfelbeck & Raess, 2008; Perez et al., 2012). In this scenario, zebra finches treated with CORT during development may respond more strongly to social isolation and learn better in

social isolation (a potentially stressful environment). Future studies could evaluate this hypothesis by testing learning in a social environment (i.e. with conspecifics present) or by directly measuring the effects of CORT treatment during development on social stress responses.

Using a food reward in learning tasks could potentially confound results because of the sustained effects of developmental stress on metabolic rate. Essentially, birds with higher metabolic rates may be more motivated to search for food and, therefore, solve the foraging task in fewer trials regardless of learning ability. However, we found that exposure to CORT during development did not affect basal metabolic rate in our sample, suggesting that differential motivation does not explain the trend for CORT-exposed birds to solve the learning task faster. Long-term metabolic effects of developmental stress vary among species studied to date (Schmidt et al., 2012; Spencer & Verhulst, 2008). Schmidt et al. (2012) found that female song sparrows exposed to restricted food or elevated CORT during the nestling period had increased standard metabolic rates as adults. In contrast, Spencer and Verhulst (2008) found that CORT treatment during the nestling period elevated standard metabolic rate in young zebra finches (12 days posthatch), but not in adult zebra finches (55–65 days posthatch). Our results closely match those described in Spencer and Verhulst (2008) using similar methods, and support the idea that incongruous results between studies could be due to different experimental methodologies.

Development stress can have broad phenotypic effects beyond what was measured in this study. For example, developmental stress can have sustained effects on neophobia (fear of novel objects). Male zebra finches exposed to developmental stress show reduced latencies to approach a novel object compared to control birds (Spencer & Verhulst, 2007). Although we found that zebra finches treated with CORT during development solved each stage of a novel foraging paradigm in fewer trials than control siblings, variation in the number of trials to solve each stage was driven entirely by variation to complete the first stage. Passing the first stage obligated the birds to interact with the foraging grid (a novel object) for the first time. Therefore, it is possible that our treatment had no effect on learning per se, but rather modulated other behaviours (i.e. neophobia), which indirectly affected the ability of birds to solve a foraging task (but see Grindstaff et al., 2012). Future studies could further investigate the interactions between neophobia and learning with comprehensive neophobia experiments and by measuring learning using methods that do not activate neophobic responses.

Substantial evidence supports the role of developmental conditions in shaping the ability of birds to learn species-specific songs. However, how generalizable the negative effects of development stress are on learning remains to be determined. The broad effects of developmental stress on phenotype could confound the outcome of learning experiments, which often rely on the use of novel objects or food rewards to assess learning ability. Future studies could account for these indirect effects by utilizing multiple learning assays, employing learning tasks that do not rely on food or novel objects, or by directly measuring possible confounding behavioural and physiological factors.

Acknowledgments

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