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Does early stress prepare individuals for a stressful future? Stress during adolescence improves foraging under threat

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Adolescent exposure to adverse environmental conditions can cause lasting changes in behaviour, cognition and physiology. One explanation for why such changes occur is that they allow organisms to adjust aspects of their phenotype to enhance function in an unfavourable environment. This concept has been investigated for stress during gestation (e.g. thrifty phenotype hypothesis, maternal mismatch hypothesis). Here, we apply these ideas within an individual's lifetime as a possible explanation for long-term phenotypic changes in response to stress during adolescence. To test whether stress during adolescence can cause phenotypic changes that prepare an animal for future threat, we exposed laboratory rats to either chronic stress or unstressed control conditions during adolescent development. After a 5-week delay, rats were assessed in a timed-foraging task under both low-threat and high-threat conditions. Chronic stress during adolescence caused long-term changes in foraging behaviours and foraging performance. In low-threat conditions, stress-exposed rats had a longer latency to begin foraging but consumed the same number of rewards as unstressed rats. However, under high-threat conditions, rats exposed to stress during adolescence began foraging sooner, made more transitions between foraging patches and consumed more rewards than unstressed rats. These results indicate that stress exposure enabled rats to forage more effectively under later novel threat, and that phenotypic changes resulting from stressful experiences during adolescence may enhance function in future high-threat environments.

Stress has long been recognized as a transformative force in many taxa (Selye & Albert, 1942; reviewed in: Armario, Escorihuela, & Nadal, 2008; Francis et al., 1996). The effects of stress depend on intensity, duration and the developmental stage at exposure (Ariza Traslaviña, de Oliveira, & Franci, 2014; Park, Zoladz, Conrad, Fleshner, & Diamond, 2008; Wingfield et al., 1998; reviewed in Lupien, McEwen, Gunnar, & Heim, 2009). For example, exposure to predation threat during early development can cause lasting phenotypic changes in wood frogs (e.g. large limbs, narrower bodies; Relyea, 2001) and song sparrows (e.g. body size; Travers, Clinchy, Zanette, Boonstra, & Williams, 2010). In laboratory rats, a single encounter with a cat can decrease later exploratory behaviour (Adamec, Blundell, & Collins, 2001), interfere with memory consolidation and retrieval (Diamond et al., 2006) and change the shape of dendrites in brain cells (Mitra, Adamec, & Sapolsky, 2009).

The experience of stress during adolescent development, an inherently plastic time when regions in the brain that regulate the hypothalamic–pituitary–adrenal (HPA) axis mature, can cause lasting changes in behaviour, cognition and physiology (Caruso, McClintock, & Cavigelli, 2014; McCormick, Mathews, Thomas, & Waters, 2010; Sterlemann et al., 2008; Weintraub, Singaravelu, & Bhatnagar, 2010; reviewed in: Lupien et al., 2009; Romeo, 2010). Evidence for lasting changes following stress during adolescence is growing (reviewed in McCormick & Green, 2012). Studies of laboratory rodents have found that adolescent stress can affect spatial navigation (via changes in the hippocampus; Isgor, Kabbaj, Akil, & Watson, 2004; McCormick et al., 2010; Sterlemann et al., 2008), enhance novelty-seeking and risk-taking behaviour (Arrant,

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Schramm-Sapyta, & Kuhn, 2013; Toledo-Rodriguez & Sandi, 2011), alter decision making (Chaby, Cavigelli, White, Wang, & Braithwaite, 2013; Irwin, 1989; Torregrossa, Xie, & Taylor, 2012), change HPA axis function (McCormick et al., 2010) and increase anxiety (Green, Barnes, & McCormick, 2012; Schmidt et al., 2007).

Several studies of the lasting effects of stress during adolescence have reported negative functional outcomes, such as impairments to memory of object locations (McCormick et al., 2012) and poor reversal learning (Han, Wang, Xue, Shao, & Li, 2011). These changes have been attributed to disruptions of development and subsequent abnormal functioning of brain regions that mature during adolescence (Toledo-Rodreguiz & Sandi, 2007). However, other studies have reported phenotypic responses to adolescent stress that appear to be beneficial, including enhanced auditory fear conditioning (Toledo-Rodreguiz & Sandi, 2007) and accelerated decision making (Chaby et al., 2015). To understand the alternative outcomes from these studies, it is important to consider the context in which these responses were assessed.

The concept that organisms can adjust aspects of their phenotype to enhance function in an unfavourable environment has been investigated for stress during gestation (e.g. thrifty phenotype: Hales & Barker, 1992; maternal mismatch hypothesis: Sheriff & Love, 2013). According to the thrifty phenotype and mismatch hypotheses, early exposure to an adverse environment will prepare individuals for a high-threat environment, but may detract from performance under low-threat conditions. The disadvantages of a mismatch between gestational and later life environment have been demonstrated using cross-fostering designs (Hales & Ozanne, 2003; reviewed in Hales, 1997), natural population cycles in snowshoe hares, *Lepus americanus* (Sheriff, Krebs, & Boonstra, 2009, 2010), and manipulations of glucocorticoid exposure during embryonic development (Love, Chin, Wynne-Edwards, & Williams, 2005; Love & Williams, 2008). Here we apply these ideas within the span of an individual lifetime as a possible explanation for long-term phenotypic changes resulting from exposure to stress during adolescence (Fig. 1). We hypothesized that adolescent-stress exposure would shape adult phenotype in a context-dependent way, by preparing animals to perform better under future threat, but decreasing performance in a mismatched, low-threat environment when compared to animals reared without stress. To our knowledge this is the first study to test the effects of early exposure to stress on performance using the same assay in different environmental conditions.

To test these ideas we exposed laboratory rats to stress during adolescence or to unstressed control conditions. After a 5-week delay, we screened adult foraging behaviours (latency to engage in foraging, number of patch visits) and foraging performance (number of rewards eaten) in both low-threat and high-threat conditions. Wild rodents adjust forging behaviours when cues of predators are present (Orrock, Danielson, & Brinkerhoff, 2004), and foraging performance can be influenced by predation conditions (Pintor & Sih, 2009; Sih, 1982; Werner & Hall, 1988). Foraging performance can affect fitness through the ability to mitigate exposure to threat (Morris & Davidson, 2000), attract mates (Keagy, Savard, & Borgia, 2009, 2011) and provision offspring (Schwagmeyer & Mock, 2008). Foraging was evaluated both with and without cues of predation, using a foraging task that permitted animals to access a familiar reward by manipulating a novel object; similar assays have been used with captive and wild animals (e.g. humans and chimpanzees, *Pan troglodytes*: Herrmann, Hernández-Lloreda, Call, Hare, & Tomasello, 2009; spotted hyaenas, *Crocuta crocuta*: Benson-Amram, Weldele, & Holekamp, 2013; satin bowerbirds, *Ptilonorhynchus violaceus*: Keagy et al., 2009; house sparrows, *Passer domesticus*: Bókony et al., 2013).

We predicted that stress during adolescence would prepare animals for future threat in a context-dependent way such that, under high-threat conditions, adolescent-stressed rats would show more active foraging behaviours (begin foraging faster, move between patches more) and enhanced foraging performance (consume more rewards) relative to unstressed rats, whereas under low-threat conditions, adolescent-stressed rats would show reduced foraging behaviours and performance. Alternatively, if stress during adolescence results in a negative functional phenotype, adolescent-stressed rats should show reduced foraging behaviours and performance under both high- and low-threat conditions.

METHODS

Animals and Housing

Male Sprague–Dawley rats ($N = 24$) were obtained at 21 days of age from Harlan Laboratory in Fredrick, Maryland, U.S.A. Following transport, rats were given 7 days to acclimate before handling and experimental procedures began. Animals were randomly assigned to pair-housing in plastic cages (20 × 26 × 45 cm) with wood chip

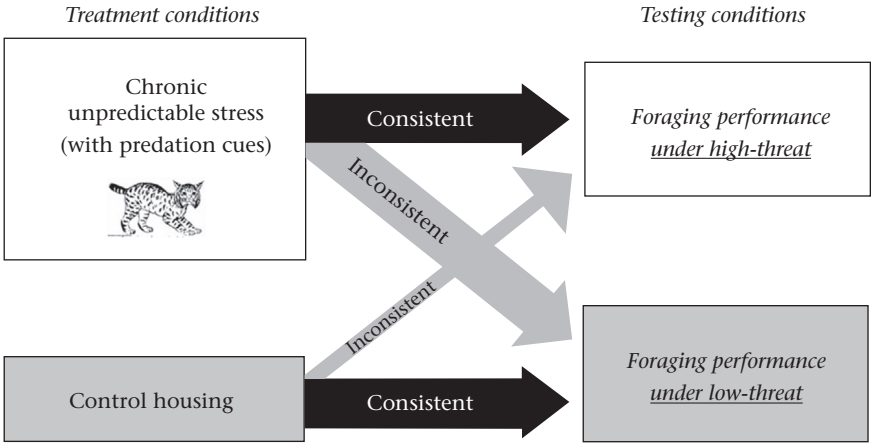

Figure 1. Framework of hypothesized performance in environmental conditions that were consistent and inconsistent with rearing (treatment) conditions. The effect of chronic unpredictable stress during adolescence on foraging performance of laboratory rats in adulthood was quantified using a seven-patch open arena foraging task under low-threat (standard conditions, under dim red light) and high-threat (visual and auditory cues of avian predation, bright white light). Stimuli used to create the high-threat testing environment were novel to both groups of rats.

bedding, two pine wood chews, and two 7.6 cm diameter PVC tubes that were suspended from the cage lid. All cages were changed weekly; wood chews and PVC tubes were replaced when visibly soiled. Standard rat chow (LabDiet® 5001, 23% protein) and tap water were available ad libitum unless otherwise noted. Rats were kept at 20–21 °C and 40–45% relative humidity on a 12:12 h reversed light:dark cycle; the dark phase was 0900–2300 hours.

To minimize disturbance, all trials were videorecorded and the experimenter was not in the room during testing. To control for circadian rhythms, tests were started a minimum of 2 h after the beginning of the dark cycle and completed within 6 h. Testing order was randomized within the adolescent-stressed and unstressed groups, and alternated between groups to control for changes in circadian rhythms. Equipment was sprayed with 70% ethanol solution and wiped clean between all trials and subjects.

Chronic Unpredictable Stress and Body Mass

Pair-housed rats were randomly assigned to either the adolescent-stress treatment ($N = 12$) or the unstressed control group ($N = 12$). Each week adolescent-stress rats between 30 and 70 days of age encountered six stressors, three during 0000–1200 hours and three during 1200–2400 hours. Stressors are described in Table 1. The three stressor types (physical, social, predation) and order of stressor presentation varied, but were balanced so that each type of stressor was represented twice per week. Variations of this stress paradigm have previously been shown to induce long-term behavioural changes (Chaby, Cavigelli, Hirrlinger, Caruso, & Braithwaite, 2015; Chaby et al., 2013). To account for handling and cage changes during the stressors, rats in the unstressed group were handled and transferred to clean cages approximately twice per week, coinciding with stressors that required a new cage. All rats were weighed weekly during the stress treatment, and every second week thereafter. Weights were monitored because body mass is a noninvasive indicator of health that can be decreased by exposure to stress in laboratory rats (e.g. noise and shocks: Pare, 1965; immobilization: Martí, Martí, & Armario, 1994; Shimizu, Oomura, & Kai, 1989; restraint: Harris et al., 1998, 2002; water avoidance: Santos, Benjamin, Yang, Prior, & Perdue, 2000; defeat in resident/intruder task: Bhatnagar, Vining, Iyer, & Kinni, 2006; but see Adam & Epel, 2007). The duration of the stress treatment (30–70 days of age) included a short postpubertal period in early adulthood (days 55–70 of treatment) to cover the entire ontogenetic window of adolescence (Schmidt et al., 2007; Sterlemann et al., 2010) and because we wanted to evaluate behaviours mediated by the prefrontal cortex (i.e. foraging, decision making; Seamans, Floresco, & Phillips, 1995), a region which continues to develop into early adulthood (Spear, 2000; Van Eden, Kros, & Uylings, 1990).

Ethical Note

Animals were housed according to the National Institutes of Health (NIH) recommendations described in the *Guide for the Care and Use of Laboratory Animals* (8th ed.). Food restriction is common in laboratory rodent studies and is advocated by NIH in order to increase longevity and decrease rates of obesity, metabolic disease, cardiovascular disease and cancer (Keenan et al., 1994; reviewed in Anderson, Shanmuganayagam, & Weindruch, 2009). During the stress treatment, no signs of pain or aggression were observed, but behavioural changes relating to the type of stressor were noted. For example, during predation stressors, increases in escape and burrowing behaviours were observed. During physical and social stressors, some avoidance behaviours were noted. For example, during exposure to damp bedding, rats spent little time in contact with the bedding and instead spent time in the PVC tubes. Following exposure to the stressors, there were no changes in aggression or health. Experiments were approved by the Pennsylvania State University Institutional Animal Care and Use Committee (IACUC protocol number 44459).

Motivation to Consume a Reward

We evaluated whether stress during adolescence influenced motivation to consume a reward in adulthood, in order to dissociate between the ability and the motivation to complete the foraging tests. Motivation was assessed at three time points: the first test was conducted for 5 min at 98 days of age, the subsequent two tests were conducted for 10 min at 99 and 104 days of age. To test motivation, rats were deprived of food for 5 h, then placed individually into empty clean cages and presented with 15 Cheerios® in a petri dish. Any Cheerio that was partially eaten or bitten was considered 'eaten' because rats often sample food items rather than consuming them whole, potentially to avoid ingesting large quantities of contaminated food (Clark, 1982). The proportion of Cheerios that were partially and completely consumed did not vary between treatment groups. All rats ate 2–12 Cheerios, indicating that the reward was palatable but not exhausted during the test, thus providing a time frame for the subsequent foraging tests. Repeated exposure to the Cheerio rewards during the motivation

Table 1
Chronic unpredictable stressor descriptions

Stressor	Description
Physical	
Smaller cage	Rat pairs were housed for 4 h in a cage with a 25% reduction in volume (Doyle et al., 2011)
Damp bedding	Rat pairs were housed for 6 h with 200 ml of water mixed into 2/3 of the bedding of the home cage (Harding, Paul, & Mendl, 2004)
Cage tilt	Home cages were tilted at a 30° angle for 6 h (Harding et al., 2004)
Social	
Isolation	Rats were housed individually for 1 h in a clean cage with a 7.6 cm diameter PVC tube and a 2.5×2.5×8 cm pine wood block (McCormick et al., 2008)
Crowding	Two pairs of rats were combined into one clean cage (20×45 cm) for 4 h (Harding et al., 2004; Doyle et al., 2011)
Foreign bedding	Experimental pairs were housed in the empty home cage of a pair of older conspecifics for 12 h (Harding et al., 2004)
Predation	
Taxidermic bobcat	An adult male taxidermic bobcat, *Lynx rufus*, was placed on a wheeled cart and moved continuously in front of rat cages for 30 min (Blumstein, Daniel, & Springett, 2004)
Fox urine	Tink's Red Fox-P® was sprayed onto cotton balls and placed into home cages for 30 min (Fendt & Endres, 2008)
Cat fur	Domestic cat, *Felis catus*, fur was placed into the home cages, inside of mesh, for 30 min (Kendig, Bowen, Kemp, & McGregor, 2011)
Feline vocalizations	Bobcat, mountain lion, *Puma concolor*, domestic cat, lion, *Panthera leo*, and tiger, *Panthera tigris*, vocalizations were played for 30 min (Chaby et al., 2015)

tests also served to familiarize the rats with Cheerios before the foraging tests, thus minimizing the potential effects of differences in novelty seeking caused by the adolescent-stress treatment (Toledo-Rodriguez & Sandi, 2011).

Foraging Tests

To determine whether stress during adolescence had long-term effects on foraging, we conducted three foraging tests, two in low-threat conditions (at 108 and 111 days of age) and one under high-threat (at 144–145 days of age). Outside of captivity, the median life span of male Norway rats is approximately 250 days (Davis, 1948, 1953). The low-threat foraging test was given twice to determine whether adolescent stress interfered with the ability to learn the foraging task. The second low-threat foraging test also screened for potential stress-induced decreases in neophobia (Chaby et al., 2013). To allow for habituation to the testing environment, 3 days prior to the first foraging test rats were placed individually in the white Plexiglas testing arena (122 × 122 × 46 cm) without rewards for 5 min. Rats were deprived of food in their home cage for 5 h before the habituation and foraging tests.

The high-threat condition was tested last because rodents often show altered behaviour when re-exposed to an environment where they have encountered a predator, even after the predator is removed (reviewed in Maren, 2001). For example, California ground squirrels, *Spermophilus beecheyi*, show similar or greater rates of vigilance and antipredator behaviour (e.g. tail flagging, aerial leaps) in an environment where they have previously seen a rattlesnake but the snake is no longer visible relative to when a snake is present (Putman & Clark, 2015). The effects of encountering a predator can be persistent; a single predator encounter can cause lasting increases in anxiety in laboratory rats (Adamec & Shallow, 1993). To minimize the effects of the low-threat tests on the high-threat test, the two testing conditions were separated by 34 days.

During the foraging tests, rats moved freely between seven objects that each concealed zero to three Cheerios to simulate a multipatch foraging scenario. The total number of Cheerios available in all foraging tests was 15. Rats consumed Cheerios ad libitum for 12 min in the first low-threat test and for 10 min in the second low-threat test and the high-threat test. Rats obtained Cheerios by manipulating objects in the arena; some objects required forepaw manipulations, such as inversion or pushing, while others could be accessed by nose poking. Certain objects required whole-body manipulations, such as climbing under an inverted bin. Objects varied in texture, colour, shape and size, and in the manipulation required to obtain the reward (Supplementary Fig. S1). Objects included green, blue and yellow plastic sand toys, plastic bins, semicircular mesh domes and a plastic pinwheel. Given that the arrangement of objects was novel in the first low-threat test (with the second low-threat test intended only to look at learning), we used a novel arrangement of objects in the high-threat test in order to compare foraging performance across novel foraging contexts. In addition, the use of novel object arrangements in the low- and high-threat tests controlled for possible differences in spatial or object memory, traits that can be affected by adolescent stress (Isgor et al., 2004; McCormick et al., 2012). Within the two low-threat tests and the high-threat test, object position, orientation and the number of available rewards were the same for all animals. Given that objects covered potential food rewards, we use the term 'patch' below to discuss the combination of object and potential food reward.

Foraging behaviours

Exposure to stress can either increase (Archard & Braithwaite, 2011) or decrease rates of activity depending on context (Faraday et al., 2002). To understand activity during the foraging task, we measured switches between patches (Heithaus, Opler, & Baker, 1974; Meyhöfer, 2001). A switch between patches was defined as visiting two patches sequentially. Patch switches likely serve many functions including foraging and exploration.

Stress can increase both vigilance (Dimond & Lazarus, 1974; Liley & Creel, 2008) and the latency to eat a familiar food (Sterlemann et al., 2008); to determine whether stress during adolescence increased the latency to forage, we measured the latency to the first patch visit. Visiting a patch was defined as physically contacting an object in the arena, or the Cheerios it concealed, with either a paw or nose. Foraging behavioural data were obtained from video recordings by an experimenter naïve to treatment.

Foraging performance

Foraging performance was defined as the number of Cheerios eaten during the timed foraging test (using the same operational definition of eaten as the motivation test). Performance was determined immediately after each foraging test by an experimenter naïve to treatment.

Low-threat and high-threat conditions

The conditions in the low- and high-threat foraging tests differed only in the addition of predation cues and brighter lighting conditions in the high-threat test. The low-threat test was conducted in dim, red light, whereas the high-threat test was conducted in standard laboratory light conditions (430 lx). Light levels as low as 60 lx can be aversive to nocturnal rodents (Bueno, Zangrossi, & Viana, 2005) and can signal heightened predation risk (Clarke, 1983; Kotler, Brown, & Hasson, 1991).

Cues of avian predators were used in the high-threat test because they were novel to both groups. Hawk vocalizations were used as acoustic predation cues (e.g. Cooper's hawk, *Accipiter cooperii*, red-tailed hawk, *Buteo jamaicensis*) and were played from an audio recorder approximately 1.5 m above the arena floor. A hawk silhouette moved over the foraging arena in a pendulum motion as a visual cue of predation. When the momentum of the silhouette stopped, it was positioned over a perch 1.5 m above the arena. The silhouette was congruent in size with the hawk predators used for the acoustic predation cues (wing span: length - × width = 47 × 95 cm; Cabe, 1993). The acoustic and visual cues began as soon as the experimenter left the testing room.

The stimuli used in the high-threat test are known to be aversive to laboratory rats (loud noise: Pearl, Walters, & Chris, 1964; suddenly moving objects: Blanchard, Mast, & Caroline, 1975; Bronstein & Hirsch, 1976; bright light: Crozier & Pincus, 1927; Keller, 1941). These cues were used to create a high-threat environment, but whether rats interpret these cues, or other simulated predators, as signals of predation or merely as aversive is debated (Griffin, Evans, & Blumstein, 2001; reviewed in Blumstein, 2006).

Data Analysis

To meet the assumption of normality, data for latency to visit a patch and number of Cheerios eaten were ln transformed. All analysed data were evaluated using Levene's test for equality of variances and conformed to the assumptions for conducting parametric analyses. Body weight data were analysed using a repeated measures analysis of variance (RMANOVA) with stress condition and time as fixed effects. Data from the three motivation tests were also analysed with a RMANOVA with stress condition and time as fixed effects. Data from the three foraging tests (latency to visit a patch, switches between patches, number of Cheerios consumed) were analysed with RMANOVAs with stress condition and time as fixed effects. If time or interaction effects were detected in the

RMANOVA, each time point was analysed individually using univariate ANOVA. One data point from the control group was omitted from the latency to visit a patch analysis because it was greater than 12 standard deviations away from the mean. Analyses were run using IBM® SPSS® Statistics (Version 21); values are reported as means ± SE. Partial eta-squared values, expressing the proportion of variance explained, are provided as effect size estimates.

RESULTS

Chronic Unpredictable Stress and Body Mass

Adolescent stress did not affect body mass ($F_{1,22} = 1.59$, $P = 0.220$, $\eta_p^2 = 0.081$). Body mass increased with age in all rats ($F_{1,22} = 4945$, $P < 0.001$, $\eta_p^2 = 0.995$). Just before the beginning of the adolescent-stress treatment, the adolescent-stressed group weighed on average 83.1 ± 2.3 g and the unstressed group weighed 81.0 ± 1.6 g. The rate of change in body mass was accelerated by stress treatment; between 30 and 75 days of age, body mass of adolescent-stressed rats increased to 346.4 ± 3.8 g while that of unstressed rats increased to 332.5 ± 6.6 g (stress∗time interaction: $F_{1,22} = 2.84$, $P = 0.008$, $\eta_p^2 = 0.108$). The groups diverged most in early adulthood, but adolescent-stressed and unstressed rats did not differ significantly in body mass at any time point (ANOVAs: $P > 0.05$). Body mass of groups converged as time from the adolescent-stress treatment increased.

Motivation to Consume a Reward

Adolescent stress did not affect motivation to consume rewards across the three motivation tests (stressed average: 6.2 ± 0.4; unstressed average: 5.2 ± 0.5; $F_{1,22} = 1.59$, $P = 0.221$, $\eta_p^2 = 0.070$). Consumption remained constant over time ($F_{1,22} = 0.90$, $P = 0.416$, $\eta_p^2 = 0.041$). Stress did not affect the rate of change in motivation to consume a reward (stress∗time interaction: $F_{1,22} = 0.46$, $P = 0.636$, $\eta_p^2 = 0.021$). Reward consumption in the adolescent-stressed and unstressed rats increasingly converged across the three motivation tests and did not differ significantly at any point (ANOVAs: $P > 0.05$).

Foraging Behaviours

Across the three foraging tests, the latency to visit a patch was not affected by adolescent-stress exposure ($F_{1,21} = 0.66$, $P = 0.451$, $\eta_p^2 = 0.012$) but did change over time ($F_{1,21} = 3.24$, $P = 0.039$, $\eta_p^2 = 0.138$). No interaction was detected (stress∗time interaction: $F_{1,21} = 1.15$, $P = 0.346$, $\eta_p^2 = 0.074$). When the foraging tests were evaluated individually, we found that during the first low-threat foraging test, adolescent-stressed rats had a 17% longer latency to visit a patch than unstressed rats ($F_{1,21} = 4.88$, $P = 0.042$, $\eta_p^2 = 0.268$; Fig. 2a); the stress treatment did not affect the latency to visit a patch during the second low-threat test or during the high-threat test ($P > 0.05$; means in Table 2).

The number of switches between patches across the three tests was not affected by stress exposure ($F_{1,22} = 1.87$, $P = 0.205$, $\eta_p^2 = 0.073$) but did change over time ($F_{1,22} = 110.55$, $P < 0.001$, $\eta_p^2 = 0.729$). There was a stress∗time interaction ($F_{1,22} = 4.06$, $P = 0.035$, $\eta_p^2 = 0.181$; Fig. 2b). During the first low-threat test, rats exposed to stress during adolescence visited 9% fewer patches than unstressed rats, but under high-threat, adolescent-stressed rats visited 20% more patches than unstressed rats. When the foraging tests were evaluated individually, no treatment effects were detected in low-threat conditions (low-threat test 1: $F_{1,22} = 3.19$, $P = 0.092$, $\eta_p^2 = 0.158$; low-threat test 2: $F_{1,22} = 0.38$, $P = 0.542$, $\eta_p^2 = 0.017$). During the high-threat test, however, adolescent-stressed rats switched patches more than unstressed rats ($F_{1,22} = 4.86$, $P = 0.039$, $\eta_p^2 = 0.188$).

Foraging Performance

The number of Cheerios eaten was affected by stress exposure across the three tests ($F_{1,22} = 5.36$, $P = 0.035$, $\eta_p^2 = 0.135$; Fig. 3) and changed over time ($F_{1,21} = 9.02$, $P = 0.001$, $\eta_p^2 = 0.230$). We found no stress∗time interaction ($F_{1,22} = 1.13$, $P = 0.338$, $\eta_p^2 = 0.094$). When the foraging tests were evaluated individually, we found that adolescent-stressed and unstressed animals did not differ in reward consumption in low-threat conditions (test 1: $F_{1,22} = 2.68$, $P = 0.121$, $\eta_p^2 = 0.023$; test 2: $F_{1,22} = 0.61$, $P = 0.442$, $\eta_p^2 = 0.27$). In high-threat conditions, however, adolescent-stress rats consumed 43% more Cheerios than unstressed rats ($F_{1,22} = 4.24$, $P = 0.050$, $\eta_p^2 = 0.171$).

DISCUSSION

We found that chronic stress exposure during adolescence and early adulthood had long-term effects on foraging under low- and high-threat conditions. Motivation to consume a reward was not altered by adolescent stress, suggesting that differences detected in the foraging task could be attributed to the ability to perform the task, rather than motivation to consume food rewards. Under low-threat conditions, exposure to adolescent stress affected foraging behaviours but not foraging performance; during the first low-threat foraging test, adolescent-stressed rats took 106% longer to visit a patch but consumed the same number of food rewards as unstressed rats. During the second low-threat foraging test, both groups improved foraging performance at the same rate, suggesting that stress during adolescence does not affect the ability to learn a foraging task. In the high-threat environment, rats previously exposed to stress during adolescence visited more patches and consumed more of the available rewards compared to unstressed rats. This suggests that stress during adolescence enhanced foraging-related problem solving under threat and supports our hypothesis that prior stress prepares adolescent-stressed animals to function better under future threat.

The effects of adolescent stress on foraging behaviours may be related to managing threat. In the first low-threat foraging test, adolescent-stressed rats showed prolonged vigilance before visiting a patch and tended to visit fewer patches compared to unstressed rats, possibly to reduce exposure to open areas (although the latter effect was nonsignificant). This suggests that stress during adolescence may heighten threat avoidance behaviours even in the absence of a direct threat. Arcis and Desor (2003) found that, under low-threat conditions, rats made foraging decisions based primarily on safety, rather than food density. Prior studies have also shown that exposure to stress during adolescence can increase the latency to eat a familiar food in a novel environment (hyponeophagia; Chaby et al., 2015; Sterlemann et al., 2008) and decrease time in open areas in an elevated plus maze in adulthood (McCormick, Smith, & Mathews, 2008; Schmidt et al., 2007; Sterlemann et al., 2008; Wilkin, Waters, McCormick, & Menard, 2012). The current results are consistent with the possibility that long-term behavioural changes resulting from adolescent stress may function to maximize threat avoidance even under low-threat conditions. Whether or not behavioural changes resulting from adolescent stress functionally deter threat, however, requires further investigation.

Animals exposed to stress during adolescence tended to maintain more consistent foraging behaviours and foraging performance across the testing conditions. The change in foraging behaviours between the first low-threat test and the high-threat test was

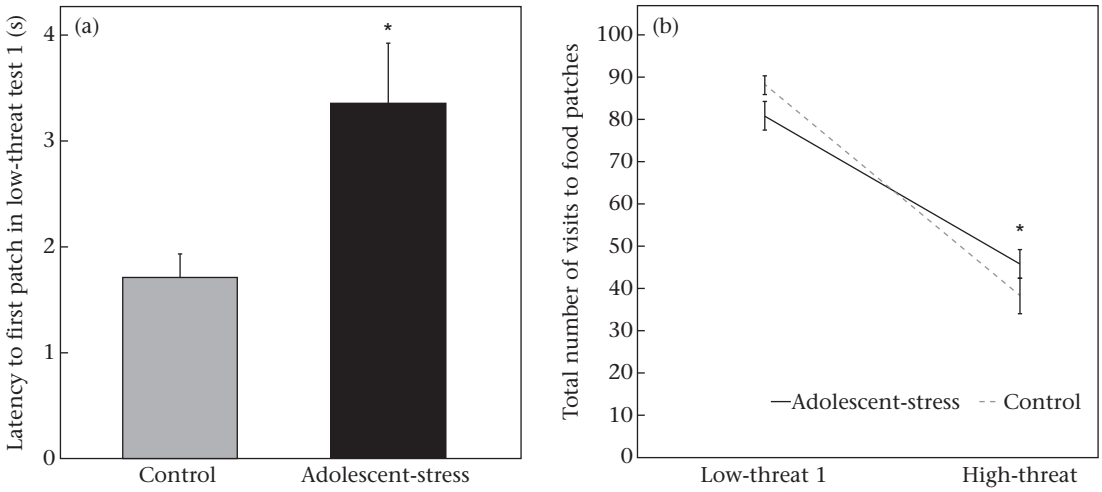

Figure 2. Effect of stress during adolescence on foraging behaviours of laboratory rats. (a) Latency to approach an object during the first low-threat test for unstressed (control) rats and adolescent-stressed rats. Plotted values are raw data, but analyses were performed on ln-transformed data. (b) Number of visits to food patches by adolescent-stressed and control rats in the first low-threat test and in the high-threat test. Values are means ± SE. $^*P = 0.05$.

Table 2
Mean ± SE latency to visit a patch by rats foraging under low-threat and high-threat conditions

	Latency to visit a patch (s)	
	Control	Adolescent-stressed
Low-threat test 1	1.7±0.3	3.5±0.7
Low-threat test 2	3.5±0.9	2.2±0.4
High-threat test	5.6±1.1	5.1±1.1

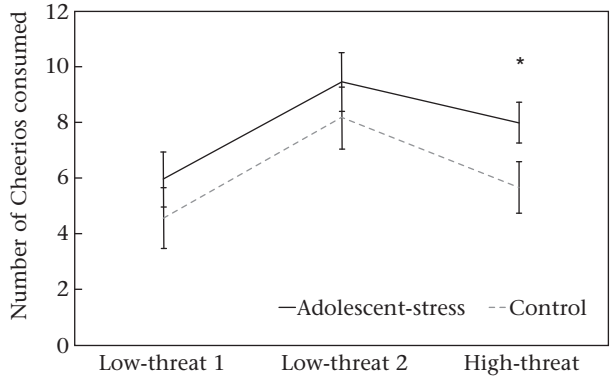

Figure 3. Effect of stress during adolescence on foraging performance of adolescent-stressed and unstressed (control) rats in low-threat tests 1 and 2, and in the high-threat test. Plotted values are raw data, but analyses were performed on ln-transformed data. Values are means ± SE. $^*P < 0.05$.

greatest in unstressed animals, both in the latency to visit a patch (unstressed: 229%; adolescent-stressed: 46%) and the number of switches between patches (unstressed: 57%; adolescent-stressed: 43%). The current design, however, did not reveal the mechanism by which stress affected foraging. At least three possible explanations could account for the apparent increased resilience in foraging behaviours and performance of adolescent-stressed rats following introduction of threat. First, following extensive exposure to stress (from 30 to 70 days of age), adolescent-stressed rats may be more familiar with the effects of the stress response, and so can adjust to functioning in a high arousal state more easily, similar to habituation to stress (Natelson et al., 1988) or physiological acclimation to temperature or oxidative stress (Arens & Cooper, 2005; Grim, Miles, & Crockett, 2010; reviewed in Romeo, 2015). Second, adolescent stress may heighten anticipation of future threat such that even under low-threat conditions, adolescent-stressed rats behave as though threat is already present or imminent. This could be mediated by a persistent high anxiety-like state (reviewed in McEwen, 2004), which is suggested to occur following stress during adolescence (Chaby et al., 2015; Green et al., 2012; Wilkin et al., 2012). Supporting this, wild mice increase antipredator foraging behaviours in response to an increase in predator density, even when predators have previously been absent for 24–28 generations (Orrock & Fletcher, 2014). A third possibility is that rats compared the high-threat cues with prior aversive stimuli they encountered, and because the adolescent-stressed rats were exposed to more extreme aversive stimuli, they interpreted the high-threat cues as less threatening. This would be similar to the psychological phenomenon of contrast effects, where exposure to high-intensity stimuli bias the perception of subsequent related stimuli as less intense (Moskowitz, 2005).

During the high-threat foraging test, unstressed rats obtained 2.8% of their daily nutrient requirements, while adolescent-stressed animals obtained 4.1% (based on 100 calories (418.58 J) per day; National Research Council (US) Subcommittee on Laboratory Animal Nutrition, 1995). Were rats to continue foraging at this pace, unstressed rats would obtain their daily nutrient requirements in 5.88 h; adolescent-stressed rats would satiate faster, in 4.12 h, potentially reducing their exposure to threat. When tested in a context consistent with their adolescent environment, adolescent-stressed rats performed better than threat-naïve rats, supporting both the mismatch and thrifty phenotype hypotheses. The increased foraging performance of adolescent-stressed rats under high-threat conditions could be explained by expanding the maternal mismatch hypothesis to address the effects of stress during development (Sheriff & Love, 2013). According to the mismatch hypothesis, maternal stress during gestation, or shortly thereafter, can cause phenotypic adjustments in offspring that are adaptive if the maternal environment predicts the offspring environment. For example, developing European starlings, *Sturnus vulgaris*, exposed to high levels of stress hormones hatch smaller and require less provisioning, and so match the quality of a challenging environment where provisioning is difficult or dangerous (Love et al., 2005; Love & Williams, 2008).

It has been suggested that adolescence is a sensitive period, like gestation, when programming can occur to prepare an individual for a specific environment (reviewed in McCormick et al., 2010). Thus, it seems that programming during adolescence may better match an individual to a future environment that is consistent with their adolescent environment.

We did not find evidence that exposure to adolescent stress decreases foraging performance in mismatched, low-threat conditions (as might be predicted by extensions of both the mismatch and thrifty phenotype hypotheses). This could indicate that rats maintain foraging performance by accepting trade-offs in the performance of other systems not evaluated here. Alternatively, stress during adolescence could affect foraging performance on a longer timescale than was evaluated here, or the design of the foraging task may not have captured existing impairments caused by stress. It is noteworthy that although the effect of stress on foraging performance was not significant under low-threat conditions, on average the adolescent-stressed rats consumed more rewards in both low-threat tests. The results from low-threat conditions do not contradict crucial early hypotheses addressing the effects of prenatal stress, but suggest that the consequences of stress during adolescent development, and their potential role in preparing for later environments, may not function by the same mechanisms as prenatal stress. This emphasizes that both the immediate and lasting effects of stress are highly dependent upon ontogenetic stage at exposure (Lupien et al., 2009).

The presence of long-term behavioural changes following adversity during adolescence may imply an expectation of environmental consistency. In the wild, Norway rats, *Rattus norvegicus*, can have relatively constant habitat conditions; they are suggested to be philopatric beyond independence (Waser & Jones, 1983), they tend to have relatively small home ranges (0.066 ha: Taylor, 1978; 0.024 ha: Villafañe, Muschetto, & Busch, 2008), and they are vulnerable to the same predators throughout ontogeny (Childs, 1986). These characteristics may contribute to the capacity for temporary periods of stress to have long-lasting effects in rats. In a species where early environment does not predict adult environment we would expect only temporary changes in phenotype following stress during development. For example, adult wood frogs, *Rana sylvatica*, require different habitats than juvenile tadpoles, and adults do not retain antipredator responses from earlier stages of development (Relyea, 2005; Relyea & Auld, 2005). Thus, it seems possible that long-term changes resulting from stress during development may be more likely in species with high environmental consistency. Evaluation of species with environmental needs that vary throughout ontogeny could reveal whether the lasting changes documented here will generalize across contexts and whether environmental consistency and the duration of behavioural changes are causally related. Furthermore, given the limited ability of laboratory systems to inform free-living systems (Koolhaas, de Boer, & Buwalda, 2006), investigation of species outside of captivity could help elucidate the biological significance of the behavioural changes described here.

The possibility that individuals can adjust phenotypic traits during adolescence in order to adjust to a persistent high-threat environment remains an attractive but incomplete story. Our results demonstrate that stress during adolescence can affect behaviour long after direct exposure to stressors has ceased and that these effects are context specific, emphasizing the importance of careful consideration of testing conditions and their relationship to environmental conditions throughout development. These findings have implications for understanding the potential functional role of stress-induced behavioural changes. They also broaden our understanding of how stress-induced phenotypic plasticity may interact with the consistency of threat across ontogeny. Our results support the idea that adolescence can be a transformative developmental stage during which environmental pressures can generate long-term behavioural changes that prepare an individual for a specific environment.

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Supplementary Material

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