



RESEARCH PAPER

Stress During Adolescence Shapes Performance in Adulthood: Context-Dependent Effects on Foraging and Vigilance

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Abstract

Exposure to chronic stress during adolescence can shape behaviour, cognition and physiology in adulthood, but the consequences of these long-term changes remain unclear. Prior studies reporting altered performance following exposure to stress in adolescence have generally interpreted lasting changes as impairments. However, we have recently shown that exposure to chronic unpredictable stress during adolescence (from post-natal days 30–70) can enhance performance in a context-dependent manner during a foraging task. Increases in foraging performance, (previously measured by the number of rewards obtained), are often associated with trade-offs in other behaviours, such as vigilance. Here, we examined the effect of stress exposure in adolescence on adult foraging in male Sprague Dawley rats to determine (1) whether the increase in foraging performance exhibited by animals exposed to stress in adolescence is balanced by a decrease in vigilance, and (2) whether stress in adolescence alters time allocation between foraging and vigilance behaviours in low- and high-threat conditions. We found no evidence of a trade-off between foraging and vigilance; under low-threat conditions, rats exposed to stress in adolescence spent more time being vigilant compared with unstressed rats, suggesting that exposure to stress in adolescence enhances anticipation of threat in adulthood. Under high-threat conditions, adolescent-stressed and unstressed rats did not differ in foraging and vigilance behaviours. Given that we have previously found that rats exposed to stress in adolescence nearly double food intake under high-threat, and we now show that high-performing rats do not spend more time foraging, it appears that stress exposure in adolescence may enhance foraging efficiency (food consumed/time) under high-threat conditions rather than time allocation between foraging and competing behaviours. We also examined the relationship, at the level of the individual, between foraging performance and foraging and vigilance behaviours. We found that changes in individual foraging performance between low- and high-threat conditions were independent of behavioural changes (i.e. both highly and poorly performing rats were equally active and contacted a similar number of patches). This suggests that the ability to obtain many rewards under high-threat conditions may be related to efficiency, rather than the frequency of foraging and effort-related behaviours.

Highlights

- 1 We compared adult foraging and vigilance behaviours in adolescent-stressed and unstressed rats.
- 2 In low threat conditions, vigilance was increased by prior exposure to stress in adolescence.
- 3 In high threat conditions, adolescent stress did not affect foraging or vigilance behaviours.
- 4 Adolescent stress may increase foraging efficiency but not effort under threat.

Introduction

Adolescence is a developmental phase characterized by a transition from dependence in early life to independence in adulthood (Spear 2000; Crone & Dahl 2012). During this phase, a myriad of physiological and neural systems mature, making adolescence a period of both plasticity and vulnerability to environmental conditions (Gogtay et al. 2004; Romeo & McEwen 2006). Exposure to adversity during adolescence can cause lasting changes in behaviour (Toledo-Rodriguez & Sandi 2011; Green et al. 2013), cognition (Chaby et al. 2013) and physiology (Romeo 2010; Caruso et al. 2014), and can affect performance in adulthood (McCormick et al. 2010). Determining the role of lasting changes in response to stress exposure in adolescence may be aided by understanding the life history context in which the experience takes place (Clinchy et al. 2011) or by understanding the functional consequences of changes resulting from adolescent-stress exposure in free-living animals. In addition, it is important to understand how the consequences of early life stress can be context-dependent (Breuner 2008; Sheriff & Love 2013).

Exposure to early stress can result in a single phenotype that performs differently depending on the environmental conditions (Oomen et al. 2010; Sheriff & Love 2013; Sheriff 2015). For example, environmental conditions can affect the ability to manipulate novel stimuli to obtain food (which is an indicator of problem-solving ability that can affect fitness; Morris & Davidson 2000; Keagy et al. 2009). Previously, we found that in high-threat conditions prior exposure to stress in adolescence enhanced the ability of rats to manipulate novel objects to obtain food (referred to as foraging performance), but in low-threat conditions foraging performance was unaffected by exposure to chronic stress in adolescence (Chaby et al. 2015a). In environments with varying levels of threat, the amount of food an animal consumes in a specific context is suggested to correlate negatively with the

amount of fear or anxiety an animal experiences at the threat level of that context (Brown 1999; Kotler et al. 2004). Here, we evaluate the effects of chronic stress in adolescence on foraging and vigilance behaviours in adulthood in high-threat conditions (exposure to a simulated predator and bright lighting conditions) and low-threat conditions (standard testing conditions).

While foraging, animals must balance time spent obtaining resources and time spent monitoring their environment for threats through vigilance (Lima & Dill 1990; Brown 1999; Brown et al. 1999; Favreau et al. 2014). Thus, to determine the effect of chronic stress in adolescence on foraging ability, it is necessary to understand both foraging performance and vigilance behaviour. It is possible that the enhanced foraging performance caused by exposure to stress in adolescence (Chaby et al. 2015a) may have an opportunity cost of reducing competing behaviours, such as vigilance (Bachman 1993). Although this is somewhat counterintuitive given the general assumption that stress exposure will increase vigilance behaviours, it is in line with predictions of the predation risk allocation hypothesis (Lima & Bednekoff 1999). The risk allocation hypothesis states that after extended exposure to stress, if patchy resources become available, animals will become more active and increase foraging even under high-threat conditions because the need for resources is too great and there are no 'better' conditions in which to forage (Sih & McCarthy 2002). Thus, we hypothesized that exposure to chronic stress in adolescence would (1) increase time spent foraging during a pulse of resource availability regardless of threat condition, and that (2) an increase in time spent foraging in high-threat conditions would have an opportunity cost of decreasing vigilance (compared with unstressed rats). The effects of adolescent stress on foraging and vigilance are likely context specific; in low-threat conditions, foraging performance is not affected by exposure to stress in adolescence (Chaby et al. 2015a), suggesting that potential trade-offs between foraging and vigilance might be unaffected by stress exposure in adolescence in the absence of threat. It should be noted that these predictions are specific to conditions with pulses of resource availability and are distinct from predictions for conditions where resources are uniform or unavailable (Ford 1983; Arditi & Dacorogna 1988). Understanding whether extended exposure to stress in adolescence can affect the relationship between threat level and time allocation may help explain the context-specific consequences of stress in adolescence.

In addition to time allocation, foraging performance may also be mediated by differences in effort or effi-

ciency (food consumed/time). We have previously found that in high-threat conditions, following testing in low-threat conditions, both unstressed rats and some rats exposed to adolescent-stress decrease their foraging performance (by up to 43%), however, some rats exposed to adolescent-stress increase their foraging performance (by up to 300%), greatly exceeding the performance of all unstressed animals and suggesting high levels of individual variation following the adolescent-stress treatment (Chaby et al. 2015a). We investigated foraging and vigilance behaviours at the level of the individual to understand the why some rats performed well under high-threat conditions while others exhibited a decrease in foraging performance. We hypothesized that a decrease in performance in high-threat conditions would be driven by reduced foraging and effort-related behaviours (reduced activity, fewer patches contacted, etc.) while an increase in performance would be driven by increases in foraging and effort-related behaviours, such that rats that exhibited minimal change in foraging behaviour across low- and high-threat conditions would show the least change in foraging performance, while animals exhibiting a decrease in foraging effort after the introduction of threat would show a decrease in foraging performance and obtain fewer rewards in the high-threat environment. Similarly, we predicted that individuals exhibiting an increase in vigilance across the threat conditions would decrease foraging related behaviours and obtain fewer rewards in the high-threat environment.

Methods

Animals and Housing

Male Sprague Dawley rats ($n = 24$) were procured at post-natal day 21 from Harlan Laboratory in Maryland. Rats were randomly assigned to pair-housing in plastic cages that contained wood chip bedding, two pine wood chews, and two 7.6-cm-diameter PVC tubes. Standard rat chow, (LabDiet[®] 5001, 23% protein) and tap water were available *ad libitum*, except preceding the behavioural trials as described below. Rats were kept on a 12:12 h reversed light:dark schedule to facilitate testing during the dark phase when rats are most active. Foraging performance data from these rats were previously reported in Chaby et al. 2015a. In this study, we report novel data on foraging and vigilance time allocation, as well as novel behavioural frequency data and data at the level of the individual, to understand whether the effects of stress in adolescence on foraging performance are mediated by trade-offs between foraging and vigilance.

Chronic Unpredictable Stress

Pairs of rats were randomly assigned to the adolescent-stress group ($n = 12$) or the unstressed control group ($n = 12$). Unstressed rats were reared in standard laboratory conditions without exposure to stress while adolescent-stressed rats were exposed to three

Table 1: Descriptions of chronic unpredictable stressors

		Duration
Physical stressors		
Smaller cage	Housed in a 25% reduced volume cage (Doyle et al. 2011)	4 h
Damp bedding	Housed with 200 ml water mixed into bedding (Harding et al. 2004)	6 h
Cage tilt	Home cage tilted at a 30° angle (Harding et al. 2004)	6 h
Social stressors		
Isolation	Individually housed with a 7.6 cm diameter PVC tube and a 2.5 cm × 2.5 cm × 8 cm pine wood block (McCormick et al. 2008)	1 h
Crowding	Two rat pairs combined into one clean cage (Harding et al. 2004; Doyle et al. 2011)	4 h
Foreign bedding	Rat pairs housed in the empty home cage of a pair of older conspecifics (Harding et al. 2004)	12 h
Predation stressors		
Taxidermied bobcat	Adult male taxidermied bobcat (<i>Lynx rufus</i>) placed on a wheeled cart and pushed in front of rat home cages (Blumstein et al. 2004)	0.5 h
Fox urine	Fox urine (Tink's Red Fox-P [®]) sprayed onto cotton balls and placed inside plastic mesh into the home cages (Fendt & Endres 2008)	0.5 h
Cat fur	<i>Felis catus</i> fur placed inside mesh into the home cages (Kendig et al. 2011)	0.5 h
Feline vocalizations	Bobcat (<i>Lynx rufus</i>), mountain lion (<i>Puma concolor</i>), domestic cat (<i>Felis catus</i>), lion (<i>Panthera leo</i>), and tiger (<i>Panthera tigris</i>) vocalizations	0.5 h

types of stressors (physical, social and predation) from 30 to 70 days of age, using procedures described in Table 1 and Chaby et al. 2014, 2015a,b. This chronic stress paradigm has been shown to cause long-term behavioural and cognitive changes (Chaby et al. 2013, 2014, 2015a). Briefly, all adolescent-stressed rats were exposed to one stressor each day (Table 1) for 6 days per week, with 1 day of rest. Within each week, adolescent-stressed rats were exposed to three stressors between 0–1200 h and three stressors between 1200–2400 h; within these blocks, the specific hour of stress exposure was randomized. Stressor order was randomized, but on average each of the three types of stressors was presented twice per week. Adolescent-stressed rats were given new home cages after predation, foreign bedding, and wet bedding stressors. To control for handling and cage changes during the stressor procedures, rats in the unstressed group were given additional handling and cage changes approximately twice per week (Kabbaj et al. 2002; Isgor et al. 2004). All rats were weighed weekly during the stress treatment, and every second week thereafter, because body mass is an indicator of health that can be decreased by exposure to adolescent-stress in laboratory rats (Pare 1965; Shimizu et al. 1989; Bhatnagar et al. 2006). The duration of the adolescent-stress treatment (30–70 days of age) included a short post-pubertal period (approx. 55–70 days of age) both to cover the entire ontogenetic window of adolescence (Schmidt et al. 2007; Sterlemann et al. 2010) and because we wanted to evaluate foraging behaviours mediated by the prefrontal cortex, which continues to develop into early adulthood (Van Eden et al. 1990; Seamans et al. 1995; Spear 2000).

Ethical Note

Housing conditions conformed to National Institute of Health (NIH) recommendations described in the Guide for the Care and Use of Laboratory Animals, 8th edition. To ensure motivation to participate, rats were food deprived for 5 h before all foraging tests. Food restriction in laboratory rodents is advocated by the NIH to increase longevity and decrease rates of obesity, metabolic disease, cardiovascular disease, and cancer (Keenan et al. 1994; reviewed in Anderson et al. 2009). During the adolescent-stress treatment, no signs of pain, aggression, or changes in health were observed. All procedures were approved by the Pennsylvania State University Institutional Animal Care and Use Committee (IACUC), protocol #44459.

Foraging Tests

Foraging was evaluated in low-threat conditions, at 108 days of age, and in high-threat conditions, at 144–145 days of age (half of the animals were tested each day, counterbalanced by treatment). To control for circadian rhythms, tests began at least 2 h after the beginning of the dark cycle and were completed within 6 h. Three days prior to the first foraging test rats were placed in an empty white Plexiglas foraging arena (122 cm × 122 cm × 46 cm) for 5 min to allow for habituation to the arena and testing room. During the subsequent foraging tests, the arena contained 15 Cheerios that were concealed by seven objects. Each object had 0–3 available Cheerios. We have previously shown that exposure to the current adolescent-stress treatment does not affect motivation to consume Cheerios (Chaby et al. 2015a).

Objects in the arena varied in texture, colour, shape, and size (e.g. green and blue plastic bins, semi-circular mesh domes). Objects also varied in the manipulation required to obtain the potential reward (e.g. forepaw manipulations, nose-poking, and whole-body manipulations such as climbing under an inverted bin). To refer to the combination of object and potential reward, we use the term 'patch' below. Rats freely consumed Cheerios in the foraging arena for 12 min in the low-threat test and 10 min in the high-threat test (to account for increases in performance related to learning across the tests). Given that the arrangement of objects was novel in the low-threat test, we used a second novel object arrangement in the high-threat test to compare performance across novel foraging contexts. The use of novel object arrangements in both the low- and high-threat tests also controlled for possible group differences in spatial or object memory, which can be affected by exposure to stress in adolescence (Isgor et al. 2004; McCormick et al. 2012). Within the low- and high-threat tests the same object position, orientation, and number of available rewards were used for all animals (see Chaby et al. 2015a sec. 2.5.1. for further discussion).

Foraging in high-threat conditions was tested last because rodents often exhibit altered behaviour when re-exposed to an environment where they previously encountered a predator, even after the predator is removed (reviewed in Maren 2001). For example, California ground squirrels exposed to an environment in which they previously saw a rattlesnake (but the snake is no longer visible) exhibit vigilance and antipredator behaviours at the same rate or greater as when a snake is present (e.g. tail flagging, aerial leaps; Putman & Clark 2015). Additionally, the effects of encountering

a predator can be persistent; a single predator encounter in a laboratory rat can cause lasting increases in anxiety (Adamec & Shallow 1993). To minimize potential effects from repeated testing, the low- and high-threat tests were separated by 34 d; rats were well into adulthood for all foraging tests, but did not approach old age (which would begin approx. 400–750 d after the final test; Pietrelli et al. 2012; Richardson et al. 2013), yet this delay may affect comparisons between low- and high-threat tests.

For the high-threat test, acoustic and visual cues of predation and bright lighting was added, but all other conditions in the low- and high-threat foraging tests were the same. The low-threat test was conducted in dim, red light, whereas the high-threat test was conducted in standard laboratory light conditions (430 lux). Light levels as low as 60 lux can be aversive to nocturnal rodents (Bueno et al. 2005) and can increase the perception of predation risk (Clarke 1983; Kotler 1984). The predation cues used in the high-threat test were novel to both the adolescent-stressed and unstressed rats to avoid potential sensitization or habituation effects from the adolescent-stress treatment. During the high-threat test, acoustic predation cues (e.g. vocalizations from

Cooper's Hawk, Red-tailed Hawk) were played from an audio recorder approx. 5 ft above the arena floor and a visual predation cue, a hawk silhouette (47 cm length \times 95 cm wingspan), was moved over the foraging arena in a pendulum motion. Although it is unclear whether the rats interpreted the hawk cues as indicators of predation or merely as aversive (Apfelbach et al. 2005), it is common to use predator models and recordings, and the stimuli used in the high-threat test are inherently aversive to laboratory rats (loud noise: Pearl et al. 1964; suddenly moving objects: Blanchard et al. 1975; Bronstein & Hirsch 1976; bright light: Crozier & Pincus 1927; Keller 1941). All trials were video-recorded, and the experimenter was not in the room during testing. Equipment was cleaned with 70% ethanol between all trials and subjects.

Foraging and vigilance behaviours

Recordings of foraging trials were analysed for foraging behaviours (number of active foraging bouts, time spent foraging) and vigilance behaviours (number of rearing bouts, time spent rearing, number of stretch attends, and number of head scans). Operational

Table 2: Operational definitions for behaviours measured during the low- and high-threat foraging tests

Behaviour measured	Operational definition
Foraging & Vigilance behaviours	
Foraging behaviours	
Time spent eating	Time extracting, manipulating, or consuming food rewards
Number of active foraging bouts	Active foraging was defined as eating or moving between patches; to qualify as a single foraging bout, foraging behaviours had to be separated by at least 5 seconds of vigilance or inactivity
Vigilance behaviours	
Time spent rearing	Time standing on two rear legs scanning the environment (Quenette 1990; Blumstein 1996; Vásquez 1997; Vásquez et al. 2002)
Number of rearing bouts	To qualify as a single rearing bout, rearing behaviours had to be separated by at least 5 seconds of vigilance or inactivity
Stretch attends ^a	Stretching of the body towards a stimulus while keeping rear legs immobile (Ribeiro-Barbosa et al. 2005)
Head scans ^a	Moving the head back and forth while keeping the body stationary (Whishaw et al. 1992; Whishaw & Kolb 2005)
Effort-related behaviours in the foraging test	
Object touches	Contacting an object in the arena with either a paw or nose
Entries into the middle of the arena	During analysis of the video-recorded trials, a transparent 8 \times 8 grid was superimposed to separate the arena into 64 equally sized squares; when a rat moved all four feet from grid squares bordering the arena walls into grid squares in the centre, it was counted as an entry into the middle
Time spent in the middle of the arena	Time in squares in the middle of the arena (Grønli et al. 2005)
Activity	Using the 8 \times 8 video analysis grid, the number of squares crossed with all four feet was quantified as a measure of activity (Candland & Nagy 1969)

^aLess than 5% of the rats exhibited stretch attends or head scans in either the low- or high- threat condition, so these behaviours were not included in subsequent analyses.

definitions are listed in Table 2). Recordings were analysed by an experimenter blind to stress condition using EthoLog[®] v. 2.2.5. (Ottoni 2000). Reward consumption data were obtained immediately after each foraging tests and were previously reported in Chaby et al. 2015a. To compare behaviour between the low- and high-threat foraging tests, we calculated the percent of time spent foraging and being vigilant by dividing the measures of time spent foraging and rearing by the length of the test.

Individual behaviour during foraging tests

We analysed, at the level of the individual, the relationship between foraging performance and foraging and vigilance behaviours within the low- and high-threat tests.

For the individual-level analysis we assessed behaviours related to foraging effort in addition to the foraging behaviours previously described. To quantify foraging effort, we measured activity (Eilam et al. 1999; Snaith & Chapman 2005), object touches (Klaassen et al. 2007), and entries and time spent in the middle of the arena (where the concentration of patches is highest; Valone & Brown 1989). Time spent in the middle of the arena has also been used as an inverse index of anxiety (Simon et al. 1994; Harris et al. 2009). We also related changes in foraging and vigilance behaviours across the low- and high-threat conditions to changes in foraging performance by calculating the percent change of all behaviours for each rat [(high-threat – low-threat)/low-threat × 100].

Data Analysis

To meet the assumption of normality, the number of active foraging bouts and the per cent of time spent rearing were natural log transformed. To confirm that the data met assumptions for parametric analyses, all data were required to pass Levene's Test for Equality of Variances. Less than 5% of the rats exhibited stretch attends or head scans in either the low- or high-threat condition, so these behaviours were not included in subsequent analyses. We tested the effect of stress in adolescence on the number of active foraging bouts, percent of time spent foraging, number of rearing bouts, and percent of time spent rearing in each threat condition at the population level using multivariate analysis of variance tests (MANOVAs) with stress condition as a main effect. MANOVAs were evaluated with Box's Test of Equality of Covariance Matrices and conformed to assumptions for parametric analyses. Dependent variables in the

MANOVAs were assessed for multicollinearity. If significant treatment effects were detected in the MANOVA, we used discriminant analysis to determine how the dependent variables contributed to the population level differences (Borgen & Selig 1978; Field 2013). At the level of the individual, to understand whether performance related to changes in behaviour between the low- and high-threat tests (independent of stress condition), we investigated the relationship between foraging performance and changes in foraging and vigilance behaviours using Pearson's correlation analyses (with a Benjamini Hochsberg correction for multiple comparisons). Analyses were run using SPSS[®] Statistics V. 21; values are reported as means ± SE.

Results

Foraging and Vigilance Behaviours

Under low-threat conditions, adolescent-stressed and unstressed rats differed in foraging and vigilance behaviours (MANOVA main effect: $F_{4,18} = 3.51$, $p = 0.031$; Fig. 1). The two vigilance variables, number of rearing bouts and percent of time spent rearing, were significantly correlated ($R = 0.86$, $p < 0.000$). This correlation between the two vigilance variables makes it difficult to isolate the effect of exposure to stress in adolescence on the vigilance variables individually and suggests that the two variables provide similar information. No other variables in the MANOVA for the low-threat condition were correlated. Discriminant analysis revealed one discriminant function encompassing all four predictors (number of active foraging bouts, percent of time spent foraging, rearing bouts, and time spent rearing), which significantly differentiated the grouping variable, stress condition, (canonical $R^2 = 0.47$, $\Lambda = 0.83$, $X^2(4) = 10.71$, $p = 0.030$, depicted in Figure S1). The discriminant function indicated that separation between the adolescent-stressed and unstressed rats was driven primarily by the adolescent-stressed rats exhibiting greater vigilance behaviours, including both greater time spent rearing (canonical variate correlation coefficients $r = 0.81$) and a greater number of rearing bouts ($r = 0.51$). This suggests that despite a close relationship between time spent rearing and the number of rearing bouts, in low-threat conditions the amount of time spent rearing distinguishes the effects of the adolescent-stress better than the number of rearing bouts. The discriminant function also showed that exposure to stress in adolescence had opposite effects on the two foraging measures; compared to

unstressed animals, adolescent-stressed rats exhibited fewer foraging bouts ($r = -0.47$), but spent a greater amount of time eating ($r = 0.34$). These effects were weaker than the effects of adolescent-stress on vigilance. Under high-threat conditions, exposure to stress in adolescence did not affect foraging and vigilance behaviours (MANOVA main effect: $F_{4,18} = 0.45$, $p = 0.770$; Fig. 1). In the high-threat foraging test, exposure to adolescent-stress did not affect either time spent foraging or being vigilant, or the number of

foraging bouts or rears. The two vigilance variables were also significantly correlated in the high-threat condition ($R = 0.69$, $p < 0.000$). No other variables in the MANOVA for the high-threat condition were correlated.

Individual Behaviours During Foraging Tests

During the low-threat foraging test, several behaviours were correlated with foraging performance

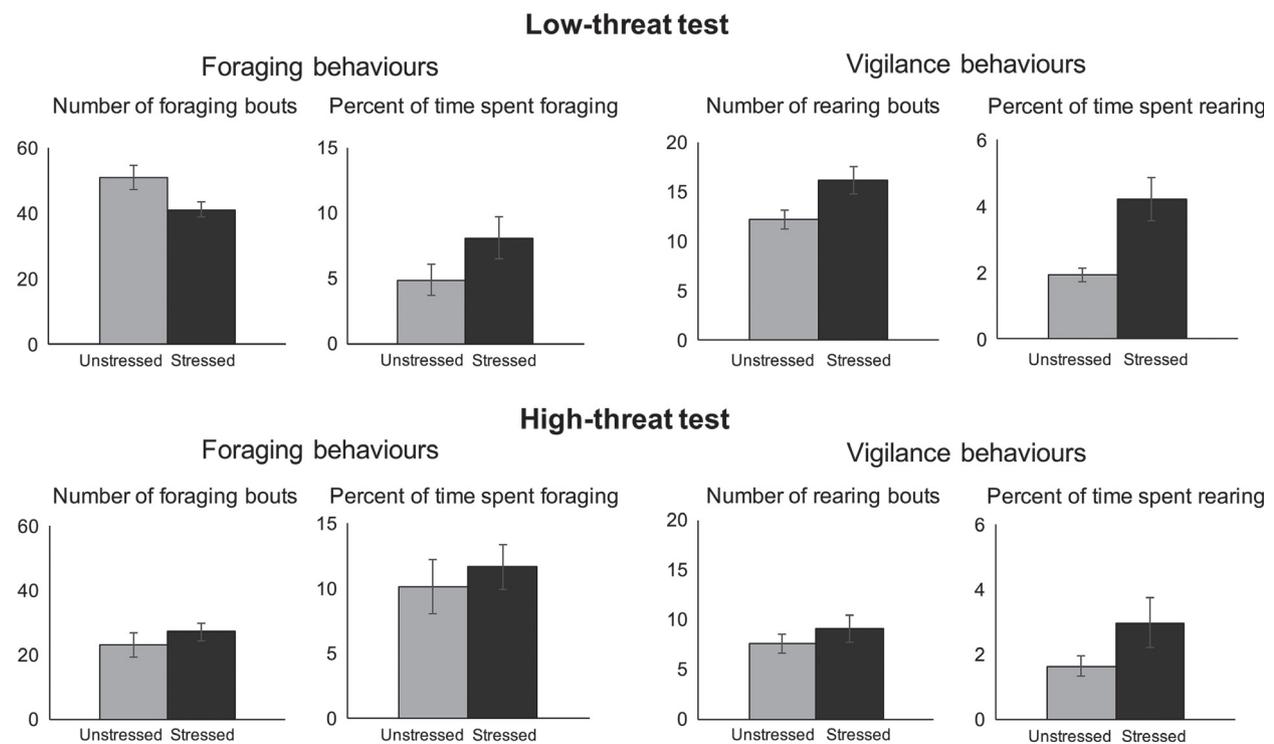


Fig. 1: The effect of chronic stress during adolescence on foraging and vigilance behaviours in low- and high-threat environments; means \pm SE. Under low-threat conditions, adolescent-stressed rats allocated time between foraging and vigilant behaviours differently compared to unstressed rats (MANOVA, $p = 0.031$). Under high-threat conditions, despite previous work showing that in high-threat conditions adolescent-stressed rats obtained more food compared to unstressed rats, here we found that adolescent-stressed and unstressed rats did not differ in foraging or vigilance behaviours, suggesting that adolescent-stressed rats obtain more food in the same amount of time compared with unstressed rats (MANOVA, $p = 0.770$).

Table 3: Correlations between behaviours and performance in the low- and high-threat tests

	Time spent foraging	Foraging bouts	Time spent rearing	Rearing bouts	Object touches	Entries into the middle	Time in the middle	Activity
Low-threat foraging performance	$R = 0.53$ $p = 0.024^a$	$R = -0.07$ $p = 0.770$	$R = -0.13$ $p = 0.622$	$R = -0.31$ $p = 0.215$	$R = 0.42$ $p = 0.077^a$	$R = 0.45$ $p = 0.032^a$	$R = 0.24$ $p = 0.313$	$R = -0.70$ $p = 0.001^*$
High-threat foraging performance	$R = 0.70$ $p = 0.001^*$	$R = 0.24$ $p = 0.253$	$R = 0.01$ $p = 0.939$	$R = -0.09$ $p = 0.680$	$R = 0.33$ $p = 0.115$	$R = -0.06$ $p = 0.766$	$R = 0.23$ $p = 0.298$	$R = -0.07$ $p = 0.740$

*Indicates significant at $p < 0.050$, with Benjamini Hochsberg correction for multiple comparisons.

^aIndicates a trend, with Benjamini Hochsberg correction for multiple comparisons.

(food consumption), including activity and strong trends for entries into the middle and time spent foraging (see Table 3). During the high-threat test, however, only the amount of time spent foraging related to foraging performance ($r = 0.70$, $p < 0.000$). Across the threat conditions, change in food consumption only correlated to change in percent of time spent foraging, and not to changes in vigilance or effort-related behaviours (see Table 4). However, changes in effort-related foraging behaviours between the low- and high-threat tests were interrelated (see Table 4). For example, rats were likely to decrease the number of patches they touched if they reduced either entries into the middle ($r = 0.56$, $p = 0.005$) or time spent in the middle of the arena ($r = 0.63$, $p = 0.002$). Similarly, animals that decreased activity across the threat conditions also decreased their entries into the middle ($r = 0.58$, $p = 0.003$). Despite these relationships, there was no correlation between the change in effort-related behaviours and the change in food consumption, which suggests that effort-related behaviours do not mediate food consumption under threat (see Table 4).

Discussion

Exposure to stress in early development can shape a phenotype such that it performs differently depending upon the environmental context (Sheriff & Love 2013; Chaby et al. 2015b). In the current study, we

tested the effects of stress in adolescence on time allocation, between monitoring for threats and manipulating novel objects to obtain food (an indicator of problem-solving ability; Keagy et al. 2009), in adulthood under low- and high-threat conditions. Under low-threat conditions, adolescent-stressed rats spent more time being vigilant and foraging, and exhibited a greater number of rearing bouts and fewer foraging bouts compared to unstressed rats. Under high-threat conditions, however, exposure to stress in adolescence did not affect the amount of time spent being vigilant or foraging, or the number of rearing or foraging bouts. Previously, we found that exposure to chronic stress in adolescence can nearly double the number of food rewards rats obtain in high-threat conditions, compared to unstressed controls (Chaby et al. 2015a). The current study showed that stress in adolescence does not affect time allocation or the frequency of foraging bouts in high-threat conditions. This suggests that in high-threat conditions, prior exposure to stress in adolescence increases foraging efficiency (food consumed/time) rather than affecting behavioural decisions on whether or not to forage. At the level of the individual, we found that foraging behaviours are related to foraging performance in low-threat conditions, but not in high-threat conditions. This indicates that it is possible for an animal to exhibit high foraging effort in high-threat conditions (e.g. frequent foraging bouts and high activity) but poor performance (few rewards obtained). Similarly,

Table 4: Percent change in behaviours across low- and high-threat conditions

	Foraging behaviours		Vigilance behaviours		Effort-related behaviours in the foraging test			
	Δ Time spent eating	Δ Number of foraging bouts	Δ Time spent rearing	Δ Number of rearing bouts	Δ Object touches	Δ Entries into the middle	Δ Time in the middle	Δ Activity
Δ Foraging performance	$R = 0.75$ $p = 0.000^*$	$R = 0.13$ $p = 0.584$	$R = -0.07$ $p = 0.760$	$R = 0.19$ $p = 0.390$	$R = 0.01$ $p = 0.963$	$R = -0.21$ $p = 0.336$	$R = -0.213$ $p = 0.330$	$R = 0.16$ $p = 0.450$
Δ Time spent eating		$R = -0.01$ $p = 0.953$	$R = -0.22$ $p = 0.927$	$R = 0.25$ $p = 0.289$	$R = 0.10$ $p = 0.752$	$R = -0.24$ $p = 0.330$	$R = -0.28$ $p = 0.234$	$R = -0.106$ $p = 0.656$
Δ Number of foraging bouts			$R = -0.28$ $p = 0.220$	$R = -0.13$ $p = 0.573$	$R = 0.15$ $p = 0.540$	$R = 0.189$ $p = 0.424$	$R = 0.29$ $p = 0.208$	$R = 0.31$ $p = 0.169$
Δ Time spent rearing				$R = 0.59$ $p = 0.005^*$	$R = 0.25$ $p = 0.282$	$R = 0.35$ $p = 0.130$	$R = 0.11$ $p = 0.625$	$R = 0.002$ $p = 0.994$
Δ Number of rearing bouts					$R = -0.05$ $p = 0.849$	$R = 0.13$ $p = 0.588$	$R = -0.02$ $p = 0.928$	$R = -0.03$ $p = 0.904$
Δ Object touches						$R = 0.56$ $p = 0.005^*$	$R = 0.63$ $p = 0.002^*$	$R = 0.30$ $p = 0.165$
Δ Entries into the middle							$R = 0.81$ $p = 0.000^*$	$R = 0.58$ $p = 0.003^*$
Δ Time in the middle								$R = 0.498$ $p = 0.016^a$

*Indicates significant at $p < 0.050$, with Benjamini Hochsberg correction for multiple comparisons.

^aIndicates a trend, with Benjamini Hochsberg correction for multiple comparisons.

changes between the low- and high-threat test in foraging behaviours (activity, contact with patches, entries in the middle of the arena, etc.) are independent of changes in the amount of food obtained. Given that differences in foraging performance cannot be attributed to changes in foraging behaviours, and given that exposure to our adolescent-stress paradigm does not affect motivation to consume food rewards in adulthood (Chaby et al. 2015a), it follows that differences in performance might be attributed to cognitive or emotional processes that interfere with the ability of a threat-naïve animal to consume food in high-threat conditions. For example, animals in anxiety-like states caused by exposure to a novel arena can exhibit hypophagia and delay reward consumption after locating a desirable food item (Merali et al. 2003; Samuels & Hen 2011).

We found that during a low-threat foraging task, adolescent-stressed rats spent more time foraging and being vigilant than unstressed rats, refuting our prediction that exposure to stress in adolescence would decrease vigilance in order to increase foraging during a pulse of resource availability. The finding that stress exposure during adolescence increases the time spent foraging, but decreases the number of foraging bouts, suggests that exposure to stress in adolescence may cause a change in strategy that is reflected by fewer, longer bouts of foraging in low-threat conditions. In Chaby et al. (2015a), we proposed that stress experienced during adolescence could cause context-specific changes in foraging, compared to animals naïve to threat, by (1) increasing familiarity and functioning in high stress states, (2) heightening anticipation of future threat even under low-threat conditions, or (3) biasing the perception of stressful stimuli as less intense (i.e. contrast effects; Moskowitz 2005). Both explanations (1) and (3) suggest that differences between adolescent-stressed and unstressed rats would be observed primarily in high-threat conditions. The current findings, that exposure to stress in adolescence does not affect foraging and vigilance behaviours in high-threat conditions but amplifies vigilance in low-threat conditions, supports explanation (2), suggesting that stress exposure in adolescence may modulate neurological processes or states that mediate threat detection to increase anticipation of threat. These changes might manifest as increased neophobia or anxiety; we have previously shown that the adolescent-stress paradigm used in the current study can cause lasting increases in anxiety-like behaviour (hyponeophagia), tested 274 d after exposure to adolescent-stress had ceased (Chaby et al. 2014).

A persistent increase in anxiety, or fearfulness, could account for the increase in vigilance that adolescent-stressed rats exhibit under low-threat conditions. If a persistent anxiety-like state could mimic the presence of a threat, it could shed light on why adolescent-stressed rats have blunted responses to an increase in threat; for example, persistent anxiety could maintain stress response systems near a threshold of response capacity. The potential role of persistent anxiety, or heightened fearfulness, following stress in adolescence is unclear; it is possible that persistent anxiety could prepare an animal for an environment where threats are common by modulating (1) the processing of threat related information (MacLeod et al. 1986; MacLeod & Mathews 1988; reviewed in Shechner et al. 2012), or (2) early threat detection and evasion (Kaviani et al. 2004; Melzig et al. 2008; Buwalda et al. 2013; reviewed in Davis 1990). Anxiety can affect threat detection processes; highly anxious rats and humans exhibit (1) a startle response with a larger amplitude (Kaviani et al. 2004; reviewed in Davis 1990), (2) increased activity of the autonomic nervous system during anticipation of threat (Melzig et al. 2008), and (3) elevated resting levels of norepinephrine, which serve as vital components of the early stress response (Mathew et al. 1981; Sevy et al. 1989). Most importantly, compared to individuals with low trait anxiety, high trait anxiety individuals (that experience pervasive anxiety outside of the context of a challenge) are biased towards threat (MacLeod et al. 1986; MacLeod & Mathews 1988) and identify threats faster (Byrne & Eysenck 1995). Exposure to threatening conditions during adolescence may trigger phenotypic changes that facilitate faster threat identification in adulthood outside of the context of a challenge.

In high-threat conditions, we found that exposure to stress in adolescence did not affect time allocation or the number of foraging and vigilance behaviours, despite previous findings that adolescent-stress increases foraging performance in high-threat conditions (Chaby et al. 2015a) for the risk allocation hypothesis (which states that after extended exposure to stress animals will forage even under high-threat conditions because there are “better” conditions in which to forage), our findings suggest that it is possible for extended exposure to threat (in the form of chronic stress in adolescence) to increase the number of resources acquired without either an opportunity cost to vigilance or an increase in time spent foraging which might increase exposure to threat. It should be noted that these effects differ markedly from changes in performance induced by acute stress, which

typically decreases foraging performance (Watson et al. 2004; Graham et al. 2010). The contrasting effects of acute and chronic stress exposure on foraging performance support assertions that extended exposure to stress can prepare an individual for subsequent stress (e.g. the Match-Mismatch hypothesis, Buwalda et al. 2013; Sheriff & Love 2013), and that the effects of stress depend on the timing and intensity of exposure.

When behaviours were analysed at the level of the individual, we found that activity and the number of patches a rat physically contacts are independent of changes in food consumption across the low- and high-threat testing conditions. Given that unstressed rats engage in the same number of foraging behaviours but consume fewer rewards in high-threat conditions compared with adolescent-stressed rats (Chaby et al. 2015a), performance under threat may relate to foraging efficiency rather than effort, suggesting that differences in performance may be attributed to cognitive processes. The capacity for chronic stress during adolescence to have lasting effects on cognition has been documented for spatial learning (Isgor et al. 2004), reversal learning (Han et al. 2011), object memory (McCormick et al. 2012), and cognitive bias (Chaby et al. 2013; reviewed in McCormick & Mathews 2010). How differences in cognition might 'scale-up' to affect performance, and how changes in performance might impact fitness, requires further investigation.

The current results suggest that stress exposure during adolescence enhances anticipation of future threat by increasing vigilance behaviours in the absence of threat. Further, in high-threat conditions, the results show that stress experienced during adolescence does not affect time allocation between foraging and vigilance. This advances our previous findings, which show that stress exposure in adolescence enhances foraging performance, and suggests that exposure to stress in adolescence enhances foraging efficiency under threat while maintaining vigilance (Chaby et al. 2015a). Our results emphasize the importance of contextualizing stress-induced changes in behaviour by testing animals in conditions consistent with their developmental environment or in conditions that reflect ecologically relevant challenges, such as predation threat or competing stimuli (Sheriff & Love 2013). The current findings both inform our understanding of the role of developmental plasticity and expand our understanding of the potential for responses to stress in adolescence to cause lasting changes in problem-solving or the capacity for divided-attention between competing goals such as monitoring threat and searching for resources.

Conflict of Interest Statement

The authors declare no conflict of interest, nor any financial or personal relationships that could inappropriately influence or bias the content of this study.

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Literature Cited

- Adamec, R. E. & Shallow, T. 1993: Lasting effects on rodent anxiety of a single exposure to a cat. *Physiol. Behav.* **54**, 101–109.
- Anderson, R. M., Shanmuganayagam, D. & Weindruch, R. 2009: Caloric restriction and aging: studies in mice and monkeys. *Toxicol. Pathol.* **37**, 47–51.
- Apfelbach, R., Blanchard, C. D., Blanchard, R. J., Hayes, R. A. & McGregor, I. S. 2005: The effects of predator odors in mammalian prey species: a review of field and laboratory studies. *Neurosci. Biobehav. Rev.* **29**, 1123–1144.
- Arditi, R. & Dacorogna, B. 1988: Optimal foraging on arbitrary food distributions and the definition of habitat patches. *Am. Nat.* **131**, 837–846.
- Bachman, G. C. 1993: The effect of body condition on the trade-off between vigilance and foraging in Belding's ground squirrels. *Anim. Behav.* **46**, 233–244.
- Bhatnagar, S., Vining, C., Iyer, V. & Kinni, V. 2006: Changes in hypothalamic-pituitary-adrenal function, body temperature, body weight and food intake with repeated social stress exposure in rats. *J. Neuroendocrinol.* **18**, 13–24.
- Blanchard, R. J., Mast, M. & Blanchard, D. C. 1975: Stimulus control of defensive reactions in the albino rat. *J. Comp. Physiol. Psychol.* **88**, 81–88.
- Blumstein, D. T. 1996: How much does social group size influence golden marmot vigilance? *Behaviour* **133**, 1133–1151.
- Blumstein, D. T., Daniel, J. C. & Springett, B. P. 2004: A test of the multi-predator hypothesis: rapid loss of antipredator behavior after 130 years of isolation. *Ethology* **110**, 919–934.

- Borgen, F. H. & Selig, M. J. 1978: Uses of discriminant analysis following MANOVA: multivariate statistics for multivariate purposes. *J. Appl. Psychol.* **63**, 689.
- Breuner, C. 2008: Maternal stress, glucocorticoids, and the maternal/fetal match hypothesis. *Horm. Behav.* **54**, 485–487.
- Bronstein, P. M. & Hirsch, S. M. 1976: Ontogeny of defensive reactions in Norway rats. *J. Comp. Physiol. Psychol.* **90**, 620–629.
- Brown, J. S. 1999: Vigilance, patch use and habitat selection: foraging under predation risk. *Evol. Ecol. Res.* **1**, 49–71.
- Brown, J. S., Laundré, J. W. & Gurung, M. 1999: The ecology of fear: optimal foraging, game theory, and trophic interactions. *J. Mammal.* **80**, 385–399.
- Bueno, C. H., Zangrossi, H. Jr & Viana, M. B. 2005: The inactivation of the basolateral nucleus of the rat amygdala has an anxiolytic effect in the elevated T-maze and light/dark transition tests. *Braz. J. Med. Biol. Res.* **38**, 1697–1701.
- Buwalda, B., Stubbendorff, C., Zickert, N. & Koolhaas, J. M. 2013: Adolescent social stress does not necessarily lead to a compromised adaptive capacity during adulthood: a study on the consequences of social stress in rats. *Neuroscience* **249**, 258–270.
- Byrne, A. & Eysenck, M. W. 1995: Trait anxiety, anxious mood, and threat detection. *Cogn. Emot.* **9**, 549–562.
- Candland, D. K. & Nagy, Z. M. 1969: The open field: some comparative data. *Ann. N. Y. Acad. Sci.* **159**, 831–851.
- Caruso, M. J., McClintock, M. K. & Cavigelli, S. A. 2014: Temperament moderates the influence of periadolescent social experience on behavior and adrenocortical activity in adult male rats. *Horm. Behav.* **66**, 517–524.
- Chaby, L. E., Cavigelli, S. A., White, A., Wang, K. & Braithwaite, V. A. 2013: Long-term changes in cognitive bias and coping response as a result of chronic unpredictable stress during adolescence. *Front. Hum. Neurosci.* **7**, 328.
- Chaby, L. E., Cavigelli, S. A., Hirrlinger, A. M., Caruso, M. J. & Braithwaite, V. A. 2014: Chronic unpredictable stress during adolescence causes long-term anxiety. *Behav. Brain Res.* **278**, 492–495.
- Chaby, L. E., Sheriff, M. J., Hirrlinger, A. M. & Braithwaite, V. A. 2015a: Does early stress prepare individuals for a stressful future? Stress during adolescence improves foraging under threat. *Anim. Behav.* **105**, 37–45.
- Chaby, L. E., Sheriff, M. J., Hirrlinger, A. M. & Braithwaite, V. A. 2015b: Can we understand how developmental stress enhances performance under future threat with the Yerkes-Dodson law? *Commun. Integr. Biol.* **8**, e1029689.
- Clarke, J. A. 1983: Moonlight's influence on predator/prey interactions between short-eared owls (*Asio flammeus*) and deermice (*Peromyscus maniculatus*). *Behav. Ecol. Sociobiol.* **13**, 205–209.
- Clinchy, M., Schulkin, J., Sheriff, M. J., McGowan, P. O. & Boonstra, R. 2011: The neurological ecology of fear: insights neuroscientists and ecologists have to offer one another. *Front. Behav. Neurosci.* **5**, 21.
- Crone, E. A. & Dahl, R. E. 2012: Understanding adolescence as a period of social-affective engagement and goal flexibility. *Nat. Rev. Neurosci.* **13**, 636–650.
- Crozier, W. J. & Pincus, G. 1927: Phototropism in young rats. *J. Gen. Physiol.* **10**, 407–417.
- Davis, M. 1990: Animal models of anxiety based on classical conditioning: the conditioned emotional response (CER) and the fear-potentiated startle effect. *Pharmacol. Ther.* **47**, 147–165.
- Doyle, R. E., Lee, C., Deiss, V., Fisher, A. D., Hinch, G. N. & Boissy, A. 2011: Measuring judgement bias and emotional reactivity in sheep following long-term exposure to unpredictable and aversive events. *Physiol. Behav.* **102**, 503–510.
- Eilam, D., Dayan, T., Ben-Eliyahu, S., Schulman, I. I., Sheffer, G. & Hendrie, C. A. 1999: Differential behavioural and hormonal responses of voles and spiny mice to owl calls. *Anim. Behav.* **58**, 1085–1093.
- Favreau, F. R., Goldizen, A. W., Fritz, H., Blomberg, S. P., Best, E. C. & Pays, O. 2014: Within-population differences in personality and plasticity in the trade-off between vigilance and foraging in kangaroos. *Anim. Behav.* **92**, 175–184.
- Fendt, M. & Endres, T. 2008: 2,3,5-Trimethyl-3-thiazoline (TMT), a component of fox odor – just repugnant or really fear-inducing? *Neurosci. Biobehav. Rev.* **32**, 1259–1266.
- Field, A. 2013: *Discovering Statistics Using IBM SPSS Statistics*, 4th edn. Sage Publications Ltd, London, UK.
- Ford, R. G. 1983: Home range in a patchy environment: optimal foraging predictions. *Am. Zool.* **23**, 315–326.
- Gluckman, P. D., Hanson, M. A. & Spencer, H. G. 2005: Predictive adaptive responses and human evolution. *Trends Ecol. Evol.* **20**, 527–533.
- Gogtay, N., Giedd, J. N., Lusk, L., Hayashi, K. M., Greenstein, D., Vaituzis, A. C., Nugent, T. F., Herman, D. H., Clasen, L. S., Toga, A. W., Rapoport, J. L. & Thompson, P. M. 2004: Dynamic mapping of human cortical development during childhood through early adulthood. *Proc. Natl Acad. Sci. USA* **101**, 8174–8179.
- Graham, L. K., Yoon, T. & Kim, J. J. 2010: Stress impairs optimal behavior in a water foraging choice task in rats. *Learn. Mem.* **17**, 1–4.
- Green, M. R., Barnes, B. & McCormick, C. M. 2013: Social instability stress in adolescence increases anxiety and reduces social interactions in adulthood in male Long-Evans rats. *Dev. Psychobiol.* **55**, 849–859.
- Grønli, J., Murison, R., Fiske, E., Bjorvatn, B., Sørensen, E., Portas, C. M. & Ursin, R. 2005: Effects of chronic mild stress on sexual behavior, locomotor activity and

- consumption of sucrose and saccharine solutions. *Physiol. Behav.* **84**, 571–577.
- Han, X., Wang, W., Xue, X., Shao, F. & Li, N. 2011: Brief social isolation in early adolescence affects reversal learning and forebrain BDNF expression in adult rats. *Brain Res. Bull.* **86**, 173–178.
- Harding, E. J., Paul, E. S. & Mendl, M. 2004: Animal behaviour: cognitive bias and affective state. *Nature* **427**, 312.
- Harris, A. P., D'Eath, R. B. & Healy, S. D. 2009: Environmental enrichment enhances spatial cognition in rats by reducing thigmotaxis (wall hugging) during testing. *Anim. Behav.* **77**, 1459–1464.
- Isgor, C., Kabbaj, M., Akil, H. & Watson, S. J. 2004: Delayed effects of chronic variable stress during peripubertal-juvenile period on hippocampal morphology and on cognitive and stress axis functions in rats. *Hippocampus* **14**, 636–648.
- Kabbaj, M., Isgor, C., Watson, S. J. & Akil, H. 2002: Stress during adolescence alters behavioral sensitization to amphetamine. *Neuroscience* **113**, 395–400.
- Kaviani, H., Gray, J. A., Checkley, S. A., Raven, P. W., Wilson, G. D. & Kumari, V. 2004: Affective modulation of the startle response in depression: influence of the severity of depression, anhedonia, and anxiety. *J. Affect. Disord.* **83**, 21–31.
- Keagy, J., Savard, J. F. & Borgia, G. 2009: Male satin bowerbird problem-solving ability predicts mating success. *Anim. Behav.* **78**, 809–817.
- Keenan, K. P., Smith, P. F., Hertzog, P., Soper, K., Ballam, G. C. & Clark, R. L. 1994: The effects of overfeeding and dietary restriction on Sprague-Dawley rat survival and early pathology biomarkers of aging. *Toxicol. Pathol.* **22**, 300–315.
- Keller, F. S. 1941: Light-aversion in the white rat. *Psychol. Rec.* **4**, 235–250.
- Kendig, M. D., Bowen, M. T., Kemp, A. H. & McGregor, I. S. 2011: Predatory threat induces huddling in adolescent rats and residual changes in early adulthood suggestive of increased resilience. *Behav. Brain Res.* **225**, 405–414.
- Klaassen, R. H. G., Nolet, B. A. & Van Leeuwen, C. H. A. 2007: Prior knowledge about spatial pattern affects patch assessment rather than movement between patches in tactile-feeding mallard. *J. Anim. Ecol.* **76**, 20–29.
- Kotler, B. P. 1984: Risk of predation and the structure of desert rodent communities. *Ecology* **65**, 689–701.
- Kotler, B. P., Brown, J. S. & Bouskila, A. 2004: Apprehension and time allocation in gerbils: the effects of predatory risk and energetic state. *Ecology* **85**, 917–922.
- Lima, S. L. & Bednekoff, P. A. 1999: Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *Am. Nat.* **153**, 649–659.
- Lima, S. L. & Dill, L. M. 1990: Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* **68**, 619–640.
- MacLeod, C. & Mathews, A. 1988: Anxiety and the allocation of attention to threat. *Q. J. Exp. Psychol. A* **40**, 653–670.
- MacLeod, C., Mathews, A. & Tata, P. 1986: Attentional bias in emotional disorders. *J. Abnorm. Psychol.* **95**, 15–20.
- Maren, S. 2001: Neurobiology of Pavlovian Fear Conditioning. *Annual Review of Neuroscience* **24**, 897–931.
- Mathew, R. J., Ho, B. T., Kralik, P., Taylor, D. L. & Claghorn, J. L. 1981: Catecholamines and monoamine oxidase activity in anxiety. *Acta Psychiatr. Scand.* **63**, 245–252.
- McCormick, C. M. & Mathews, I. Z. 2010: Adolescent development, hypothalamic-pituitary-adrenal function, and programming of adult learning and memory. *Prog. Neuropsychopharmacol. Biol. Psychiatry* **34**, 756–765.
- McCormick, C. M., Smith, C. & Mathews, I. Z. 2008: Effects of chronic social stress in adolescence on anxiety and neuroendocrine response to mild stress in male and female rats. *Behav. Brain Res.* **187**, 228–238.
- McCormick, C. M., Mathews, I. Z., Thomas, C. & Waters, P. 2010: Investigations of HPA function and the enduring consequences of stressors in adolescence in animal models. *Brain Cogn.* **72**, 73–85.
- McCormick, C. M., Thomas, C. M., Sheridan, C. S., Nixon, F., Flynn, J. A. & Mathews, I. Z. 2012: Social instability stress in adolescent male rats alters hippocampal neurogenesis and produces deficits in spatial location memory in adulthood. *Hippocampus* **22**, 1300–1312.
- Melzig, C. A., Michalowski, J. M., Holtz, K. & Hamm, A. O. 2008: Anticipation of interoceptive threat in highly anxiety sensitive persons. *Behav. Res. Ther.* **46**, 1126–1134.
- Merali, Z., Levac, C. & Anisman, H. 2003: Validation of a simple, ethologically relevant paradigm for assessing anxiety in mice. *Biol. Psychiatry* **54**, 552–565.
- Morris, D. W. & Davidson, D. L. 2000: Optimally foraging mice match patch use with habitat differences in fitness. *Ecology* **81**, 2061–2066.
- Moskowitz, G. B. 2005: *Social Cognition: Understanding Self and Others*. Guilford Press, New York, NY. 417 pp.
- Oomen, C. A., Soeters, H., Audureau, N., Vermunt, L., van Hasselt, F. N., Manders, E. M. M., Joëls, M., Lucassen, P. J., Krugers, H. 2010: Severe early life stress hampers spatial learning and neurogenesis, but improves hippocampal synaptic plasticity and emotional learning under high-stress conditions in adulthood. *J. Neurosci.* **30**, 6635–6645.
- Otoni, E. B. 2000: EthoLog 2.2 – a tool for the transcription and timing of behavior observation sessions. *Behav. Res. Methods Instrum. Comput.* **32**, 446–449.

- Pare, W. P. 1965: Stress and consummatory behavior in the albino rat. *Psychol. Rep.* **16**, 399–405.
- Pearl, J., Walters, G. C. & Chris, D. 1964: Suppressing effects of aversive stimulation on subsequently punished behaviour. *Can. J. Psychol.* **18**, 343–355.
- Pietrelli, A., Lopez-Costa, J., Goñi, R., Brusco, A. & Basso, N. 2012: Aerobic exercise prevents age-dependent cognitive decline and reduces anxiety-related behaviors in middle-aged and old rats. *Neuroscience* **202**, 252–266.
- Putman, B. J. & Clark, R. W. 2015: The fear of unseen predators: ground squirrel tail flagging in the absence of snakes signals vigilance. *Behav. Ecol.* **26**, 185–193.
- Quenette, P. Y. 1990: Functions of vigilance behaviour in mammals: a review. *Acta Oecol.* **11**, 801–818.
- Ribeiro-Barbosa, E. R., Canteras, N. S., Cezário, A. F., Blanchard, R. J. & Blanchard, D. C. 2005: An alternative experimental procedure for studying predator-related defensive responses. *Neurosci. Biobehav. Rev.* **29**, 1255–1263.
- Richardson, B. D., Ling, L. L., Uteshev, V. V. & Caspary, D. M. 2013: Reduced GABAA receptor-mediated tonic inhibition in aged rat auditory thalamus. *J. Neurosci.* **33**, 1218–1227.
- Romeo, R. D. 2010: Pubertal maturation and programming of hypothalamic–pituitary–adrenal reactivity. *Front. Neuroendocrinol.* **31**, 232–240.
- Romeo, R. D. & McEwen, B. 2006: Stress and the adolescent brain. *Ann. N. Y. Acad. Sci.* **1094**, 202–214.
- Samuels, B. A. & Hen, R. 2011: Novelty-suppressed feeding in the mouse. In: *Mood and Anxiety Related Phenotypes in Mice*, Vol. 63 (Gould, T. D., Ed.). Humana Press, Totowa, pp. 107–121.
- Schmidt, M. V., Sterlemann, V., Ganea, K., Liebl, C., Alam, S., Harbich, D., Greetfeld, M., Uhr, M., Holsboer, F., Müller, M. B. 2007: Persistent neuroendocrine and behavioral effects of a novel, etiologically relevant mouse paradigm for chronic social stress during adolescence. *Psychoneuroendocrinology* **32**, 417–429.
- Seamans, J. K., Floresco, S. B. & Phillips, A. G. 1995: Functional differences between the prelimbic and anterior cingulate regions of the rat prefrontal cortex. *Behav. Neurosci.* **109**, 1063–1073.
- Sevy, S., Papadimitriou, G. N., Surmont, D. W., Goldman, S. & Mendiewicz, J. 1989: Noradrenergic function in generalized anxiety disorder, major depressive disorder, and healthy subjects. *Biol. Psychiatry* **25**, 141–152.
- Shechner, T., Britton, J. C., Pérez-Edgar, K., Bar-Haim, Y., Ernst, M., Fox, N. A., Leibenluft, E., Pine, D. S. 2012: Attention biases, anxiety, and development: toward or away from threats or rewards?. *Depress. Anxiety* **29**, 282–294.
- Sheriff, M. J. 2015: The adaptive potential of maternal stress exposure in regulating population dynamics. *J. Anim. Ecol.* **84**, 323–325.
- Sheriff, M. J. & Love, O. P. 2013: Determining the adaptive potential of maternal stress. *Ecol. Lett.* **16**, 271–280.
- Shimizu, N., Oomura, Y. & Kai, Y. 1989: Stress-induced anorexia in rats mediated by serotonergic mechanisms in the hypothalamus. *Physiol. Behav.* **46**, 835–841.
- Sih, A. & McCarthy, T. M. 2002: Prey responses to pulses of risk and safety: testing the risk allocation hypothesis. *Anim. Behav.* **63**, 437–443.
- Simon, P., Dupuis, R. & Costentin, J. 1994: Thigmotaxis as an index of anxiety in mice. Influence of dopaminergic transmissions. *Behav. Brain Res.* **61**, 59–64.
- Snaith, T. V. & Chapman, C. A. 2005: Towards an ecological solution to the folivore paradox: patch depletion as an indicator of within-group scramble competition in red colobus monkeys (*Ptilocolobus tephrosceles*). *Behav. Ecol. Sociobiol.* **59**, 185–190.
- Spear, L. P. 2000: The adolescent brain and age-related behavioral manifestations. *Neurosci. Biobehav. Rev.* **24**, 417–463.
- Sterlemann, V., Rammes, G., Wolf, M., Liebl, C., Ganea, K., Müller, M. B. & Schmidt, M. V. 2010: Chronic social stress during adolescence induces cognitive impairment in aged mice. *Hippocampus* **20**, 540–549.
- Toledo-Rodriguez, M. & Sandi, C. 2011: Stress during adolescence increases novelty seeking and risk-taking behavior in male and female rats. *Front. Behav. Neurosci.* **5**, 17.
- Valone, T. J. & Brown, J. S. 1989: Measuring patch assessment abilities of desert granivores. *Ecology* **70**, 1800–1810.
- Van Eden, C. G., Kros, J. M. & Uylings, H. B. 1990: The development of the rat prefrontal cortex. Its size and development of connections with thalamus, spinal cord and other cortical areas. *Prog. Brain Res.* **85**, 169–183.
- Vásquez, R. A. 1997: Vigilance and social foraging in *Octodon degus* (Rodentia: Octodontidae) in central Chile. *Rev. Chil. Hist. Nat.* **70**, 557–563.
- Vásquez, R. A., Ebensperger, L. A. & Bozinovic, F. 2002: The influence of habitat on travel speed, intermittent locomotion, and vigilance in a diurnal rodent. *Behav. Ecol.* **13**, 182–187.
- Watson, R. T., Mathis, A. & Thompson, R. 2004: Influence of physical stress, distress cues, and predator kairomones on the foraging behavior of Ozark zigzag salamanders, *Plethodon angusticlavius*. *Behav. Process.* **65**, 201–209.
- Whishaw, I. Q. & Kolb, B. 2005: *The Behavior of the Laboratory Rat: A Handbook with Tests*. Oxford Univ. Press, New York, NY. 217 pp.
- Whishaw, I. Q., Dringenberg, H. C. & Comery, T. A. 1992: Rats (*Rattus norvegicus*) modulate eating speed and vigilance to optimize food consumption: effects of cover, circadian rhythm, food deprivation, and individual differences. *J. Comp. Psychol.* **106**, 411–419.

Supporting Information

Additional supporting information may be found in the online version of this article:

Table S1. Foraging behaviour data in the low and high-threat tests (mean \pm SE)

Figure S1. Discriminant scores for unstressed and stressed rats in low-threat conditions (A).