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ORIGINAL ARTICLE

Coping with style: individual differences in responses to environmental variation

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Abstract

Between-individual differences in coping with stress encompass neurophysiological, cognitive and behavioural reactions. The coping style model proposes two alternative response patterns to challenges that integrate these types of reactions. The "proactive strategy" combines a general fight-or-flight response and inflexibility in learning with a relatively low HPA (hypothalamic–pituitary–adrenal) response. The "reactive strategy" includes risk aversion, flexibility in learning and an enhanced HPA response. Although numerous studies have investigated the possible covariance of cognitive, behavioural and physiological responses, findings are still mixed. In the present study, we tested the predictions of the coping style model in an unselected population of bank voles (*Myodes glareolus*) ($N = 70$). We measured the voles' boldness, activity, speed and flexibility in learning and faecal corticosterone metabolite levels under three conditions (holding in indoor cages, in outdoor enclosures and during open field test). Individuals were moderately consistent in their HPA response across situations. Proactive voles had significantly lower corticosterone levels than reactive conspecifics in indoor and outdoor conditions. However, we could not find any co-variation between cognitive and behavioural traits and corticosterone levels in the open field test. Our results partially support the original coping style model but suggest a more complex relationship between cognitive, behavioural and endocrine responses than was initially proposed.

Significance statement

Understanding the proximate mechanisms regulating the individual variation in responses to environmental challenges and changes is fundamental in ecological and evolutionary research. Theory predicts correlations between behavioural, cognitive and physiological traits to form alternative strategies named coping styles but recent studies report contrasting and mixed findings. We examined the relationship between a measure of endocrine state (concentrations of faecal glucocorticoid metabolites), two behavioural traits (boldness and activity) and two cognitive traits (speed and flexibility of learning) in 70 unselected bank voles (*Myodes glareolus*) under three different conditions. The findings partially support the original coping style model's hypothesis and predictions. We found individual consistency of all traits. However, correlations between behavioural and cognitive aspects and endocrine state were found only in two of the three tested conditions, highlighting the need for further investigations and testing of theory.

Keywords Coping styles · Faecal glucocorticoid metabolites · Learning · Stress · Personality · Rodent

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Introduction

An individual's response to social and environmental challenges (i.e. stress, Koolhaas et al. 2011; LaDage 2015) influences its short- and long-term prospects of fitness via rank (e.g. Blanchard et al. 2001; Sapolsky 2004), reproductive success (e.g. Holberton and Wingfield 2003; Buchanan et al. 2013), as well as its risk of cardiovascular diseases, depression-like diseases and immunodeficiency (e.g. Sgoifo et al. 2005; Henry and Stephens 1977). How successfully an individual copes with challenges and changes has therefore relevance for individual fitness (e.g. Naguib et al. 2006; Cyr and Romero 2007; Maestripieri and Hoffman 2011; Razzoli et al. 2018). Adaptive responses encompass behavioural, cognitive and neuroendocrine adjustments that will enable the individual to respond while maintaining organismal functioning (e.g. Wingfield 2006; Øverli et al. 2007; Romero et al. 2009; McEwen and Wingfield 2010; Houslay et al. 2018). However, there is no single optimal way to respond to challenges. Koolhaas et al. (1999) described alternative response patterns, named coping styles, in reaction to a stressor, which integrate neuroendocrine, cognitive and behavioural traits and place individuals along a proactive-reactive axis. Proactive individuals are characterised by behavioural traits such as aggressiveness, boldness, neophilia and a general fight-flight response (Koolhaas et al. 1999; Carere et al. 2010). They are also expected to display cognitive traits such as quickly forming routines and being relatively insensible to environmental change; they would be challenged in reversal learning tasks as well as aversion learning (e.g. Benus et al. 1990; Koolhaas et al. 1999; Carere et al. 2010; de Lourdes Ruiz-Gomez et al. 2011; Sih and Del Giudice 2012). The reactive strategy instead combines low aggressiveness, risk aversion, neophobia and flexibility, as well as freezing behaviour in response to stress (e.g. Koolhaas et al. 1999; Carere et al. 2010). Reactive individuals are highly sensitive to environmental cues and changes, and quickly learn avoidance and reversal tasks (e.g. Benus et al. 1990; Koolhaas et al. 1999; Carere et al. 2010; de Lourdes Ruiz-Gomez et al. 2011; Sih and Del Giudice 2012). These patterns could be considered basic personality traits (e.g. Carere et al. 2010), defined as between-individuals differences in behaviour consistent across time and contexts (Réale et al. 2007). These suites of traits were shown to correlate with different physiological responses. Compared with reactive individuals, individuals displaying proactive behavioural and cognitive traits often have lower basal levels of glucocorticoids (e.g. cortisol or corticosterone) and lower increases in these hormones under challenging conditions than reactive individuals (e.g. Carere and van Oers 2004; Cockrem 2007; Koolhaas et al. 2010). At the same time, they show a stronger sympathetic activation in terms of plasma noradrenaline and adrenaline (e.g. Koolhaas et al. 1999) and a higher heart and breathing rate (e.g. Koolhaas et al. 1999; but see van Reenen et al. 2005; Ferrari et al. 2013).

Although the coping style model was supported, completely or partially, by several studies proving consistent individual differences in stress response strategies (reviewed in Carere et al. 2010), the adaptive value and evolutionary maintenance of such different phenotypes are still under debate (Carere et al. 2010). Furthermore, the relationship between cognitive and personality traits and the HPA (hypothalamic–pituitary–adrenal) axis is still not clear. Recent studies found no evidence of direct co-variation between responses to challenges and personality or cognitive traits as initially proposed by the coping style model (e.g. van Reenen et al. 2005; Boulton et al. 2015; Bebus et al. 2016; Qu et al. 2018; Razzoli et al. 2018). Besides, only a few studies assessed the repeatability and consistency of the behavioural, cognitive and physiological responses to stress (but see Ellis et al. 2004; Sebire et al. 2007; Ferrari et al. 2013; Boulton et al. 2015; Qu et al. 2018), which are a prerequisite for any kind of among-individual variation assessment (e.g. Dingemanse et al. 2010). Lastly, only a few recent studies (e.g. Ferrari et al. 2013; Boulton et al. 2015; Bebus et al. 2016; Qu et al. 2018) measuring differences in stress response considered wild, free-roaming or unselected populations and their results suggest a more complex relationship between the behavioural, cognitive and physiological domains. Furthermore, most of these studies report a continuous variation of traits along a proactive-reactive gradient, rather than a distinct categorisation of individuals as seen in selected laboratory lines (e.g. Wilson et al. 1994; Koolhaas et al. 1999; Brockmann 2008).

The aim of this study was to investigate the relationships between cognitive and behavioural traits consistent with a proactive-reactive axis and HPA axis reactivity in an unselected population. Our study species was the bank vole (*Myodes glareolus*), a small rodent common in central and northern Europe (e.g. Spitzenberger, 1999). Bank voles display repeatable personality and physiological traits (e.g. Labocha et al. 2004; Korpela et al. 2010; Eccard et al. 2011; Mazza et al. 2018; Schirmer et al. 2019) and some indication of co-variation between the two was recently reported (e.g. Šíchová et al. 2014). Personality in bank voles is also related to cognitive aspects such as learning speed and flexibility (e.g. Mazza et al. 2018). Here, we expanded our previous work on the relationship among personality, learning and flexibility to investigate whether behavioural, cognitive and endocrine profiles were integrated in a manner consistent with the coping style model. We measured the voles' faecal corticosterone metabolite (FCM) levels related to the challenges induced by three different environmental conditions: indoor in cages, outdoor in semi-natural enclosures and after the open field test.

The analysis of corticosterone metabolites excreted via faeces is a non-invasive and feedback-free technique to assess the adrenocortical response as a function of stress (Touma et al.

2003), and has recently been validated also for bank voles (Sipari et al. 2017). The measured stress response can thus be disentangled from the stress associated with capturing and handling the animals when collecting the sample (e.g. Palme 2019). The method is sensitive enough to detect the stress response associated with brief acute stressors as well as prolonged chronic stress, i.e. the exposure to a novel environment (e.g. Harper and Austad 2000; Bosson et al. 2009; Eccard et al. 2011; Sheriff et al. 2011; Fauteux et al. 2017).

We predicted that individuals show consistent endocrine profiles across different stress situations, i.e. endocrine profiles to be repeatable across contexts. We also predicted that individuals with proactive traits (i.e. bold, active, fast but inflexible in learning) show lower HPA axis activity and reactivity compared to individuals with more reactive-like traits (i.e. shyer, less active, slower and more flexible in learning).

Methods

Animals and housing

We used 86 captive-bred voles (45 males and 41 females), born of parents that were either wild-caught or removed from the wild for 1 to 4 generations, thus representative of their natural source population. A maximum of four individuals from the same litter (two males and two females) was included in our sample. At 3–5 weeks of age, juveniles were weaned, sexed and assigned a unique identity that was reported on the cage/enclosure at all times. From then on, animals were housed and tested individually.

Indoor conditions

Animals were housed in standard polycarbonate cages (Typ III, Ehret GmbH, Germany; dimensions: 42 cm × 27 cm × 16 cm). Light, temperature and humidity mirrored the natural conditions occurring outside the lab. Cages were provided with wood shavings and hay as bedding, and cardboard rolls for shelter. Water and food pellets (Ssniff V1594 R/M-H Ered II, Germany) were available ad libitum. Bedding was changed every 2 weeks.

Association learning and reversal learning tests

A detailed description of testing procedures is provided in Mazza et al. (2018). Briefly, we tested the voles for their olfactory associative learning speed and flexibility in a reward contingency. The test consisted of two tasks: an initial learning task and a reversal learning task. The cues were neutral odours that are not normally present in the voles' natural environment. The reward was the chance to return to the safety of the home cage through an opening in a Y-maze. The Y-maze had bent arms, so that the animals could not see from where they were released which arm ended in a blocked door and which lead to the opening. The side of the open door and associated positive cue were alternated each time a vole entered the maze, to avoid arm bias effects. For reversal learning, we switched the reward contingency, so that the previously rewarded odour now led to the blocked door. This required the animal's attention to external cues and flexible updating of the response to changed conditions; it was therefore considered a measure of cognitive and behavioural flexibility. Both tasks were considered successfully solved when the vole learned the association between the neutral odour cue and the reward, and chose the arm leading to the home cage in seven out of 10 consecutive trials. Learning and reversal learning were expressed as scores based on the number of trials necessary to reach the criterion in the two tasks.

Personality assessment

We tested for consistent between-individual differences using two standardised behavioural tests (Réale et al. 2007): the open field test and the novel object test. Voles were tested between 20 and 50 weeks of age, 2 days after the conclusion of the learning trials (see timeline in the Supplementary material). Both tests were repeated after 15 days to calculate repeatability of the behavioural response. A detailed description of testing procedures is provided by Mazza et al. (2018). The open field test (Archer 1973) is one of the most widely used tests in personality research to measure activity and exploration (Réale et al. 2007). However, it was originally introduced to measure anxiety-related behaviours, exploiting the natural aversion of rodents of exposed spaces (e.g. Archer 1973; Carola et al. 2002; Lecorps et al. 2016). Previous studies have used this test as stressor to measure not only exploratory behaviour but also physiological responses to induced stress (e.g. Bats et al. 2001; Boulton et al. 2015; Lecorps et al. 2016). A novel, empty, circular arena (100 cm wide, walls 40 cm high) was virtually divided into two areas (Herde and Eccard 2013; Mazza et al. 2018): a peripheral area of 10 cm width, and a central area of 80 cm width. Each animal was placed in the peripheral area of the arena and its behaviour was observed and recorded via a video camera (Logitech Quick Cam Pro 9000, PID LZ727BA, Logitech international S.A., Morges, Switzerland) for 10 min. From these videos, we quantified the following variables: (i) the latency to enter the central area for the first time (with the full body, excluding the tail), (ii) the proportion of time spent the central area assessed instantaneously every 10 s and (iii) the proportion of time spent active (i.e. walking, running or jumping) assessed instantaneously every 10 s. We took subjects from their home cage only during their active phase (e.g. Ylönen 1988), i.e. when they were perceived moving in the cage; this allowed us to test all animals during similar activity levels.

We assessed the animals' approach towards a novel object that was introduced in the home cage, which is usually considered a measure of boldness and neophilia (e.g. Réale et al. 2007; Crane and Ferrari 2017). We used two different novel objects, one for each round of testing: a plastic toy horse (8 × 4 × 6 cm) and a plastic toy duck (6.5 × 5 × 6 cm). The subjects' behaviour was monitored with a video camera (as above) for 30 min. We quantified the following variables from the videos: (i) the latency to leave the shelter (full body, excluding tail), (ii) the latency to approach the novel object (advancing the head closer than 2 cm), (iii) the number of interactions with the novel object (sniffing, touching and nibbling) and (iv) the overall duration of the interactions. These variables were then reduced and summarised with principal component analyses (PCA). We ran PCAs for the open field and the novel object test separately. PCA gave a composite score for each round of testing of the open field and for each round of testing of the novel object. We then calculated the individual mean PCA scores for the first factor for the open field and the novel object tests, respectively. These average scores were termed "activity" and "boldness" and used for all further analyses (further details in Mazza et al. 2018).

Outdoor conditions

A subsample of 48 voles was also tested in outdoor conditions 2–4 months after the conclusion of the indoor and open field assessments, between June and September 2016 (see Supplementary material). For this part of the experiment, we selected the animals which showed the most pronounced proactive and reactive traits, i.e. had the highest and lowest boldness and activity scores, and were the fastest and slowest to reach the criterion in an association learning test. The change from indoor to outdoor, semi-natural conditions was intended to detect possible different reactions to the challenge of adjusting to an unfamiliar environment. We tried to recreate as much as possible the characteristics and challenges of bank voles' natural environment without actually releasing them in the wild, which would have decreased our chances of retrieving them due to predation and dispersal. Voles were kept individually in 3 × 4 m semi-natural enclosures, which had a concrete base filled with a 40 cm soil layer, mesh wire walls and a plastic roof cover to provide protection from unfavourable weather and comparable conditions for all animals. Enclosures were located close to agricultural fields at the Julius Kühn Institute in Münster. They were sown with a local grass mix to mimic perennial grassland. Vegetation height was kept at ca. 2 cm in one half of the enclosures and ca. 20 cm in the other half, which was additionally covered by camouflage netting, in order to mimic the heterogeneous conditions and exposure voles might experience in their natural habitat. In each enclosure, a plastic nest box (32 × 22 × 16 cm) provided with hay was buried level with the enclosure surface in one corner to provide a nesting opportunity. Food was provided in plastic trays (20 × 15 × 5 cm) containing a mixture of crushed hazelnuts (2 g) and sand (0.75 l), so that voles would have to actively search for it. Voles remained in the enclosures for 5 days. They were then retrieved using Ugglan multiple-capture live-traps (Ugglan Special Traps n. 2, Grahnab AB, Hillerstorp, Sweden).

Faecal samples collection

Faecal pellets were collected following procedures by Liesenjohann et al. (2013) and Gracceva et al. (2014) to determine FCM concentrations that reflected basal values for holding conditions in indoor cages and outdoor enclosures and values during the second round of open field tests (see Supplementary material). Voles were tested in the open field arena between 08:00 am and 10:00 am. They were then transferred from the arena into plastic cages with mesh floor (20 × 39 × 15 cm). The cages were provided with the usual food and water and a cardboard shelter that allowed faecal pellets to drop through the bottom of the cage into a plastic tray lined with paper towels. This allowed us to easily collect them without moving, handling and therefore stressing the animals. Paper towels were changed after sampling and whenever they were stained with urine. Voles remained in the cages for ca. 8 h.

In bank voles, corticosterone metabolites take about 6–8 h to complete the passage through the intestinal tract and to be excreted with the faeces (Sipari et al. 2017). We collected the faecal pellets excreted within the first 2 h after the open field test, and considered them as indicative of the conditions the animals experienced approximately 6–8 h before (Sipari et al. 2017), which we presumed to represent undisturbed basal indoor conditions. We then collected the pellets excreted 6–8 h after the open field test and considered them indicative of the stress response to the open field test (Sipari et al. 2017). Of the 86 tested animals, 72 produced the quantity required for analyses (ca. 15–20 faecal pellets). This quantity, once dried and homogenised, allowed collecting a 0.05 g aliquot of sample. We collected the outdoor samples after retrieving the voles from the enclosures (see Supplementary material). Traps were equipped with sensors that allowed us to retrieve the voles immediately after capture (Notz et al. 2017). The glucocorticoid metabolites measured in their faeces should therefore reflect the outdoor conditions voles were experiencing in the enclosures. Voles were trapped between 08:30 am and 12:00 pm. Samples were collected within the first 2.5 h after capture. The vole was then transferred to a normal cage with hay and bedding (see "Indoor housing conditions" above). Six of 48 voles did not produce enough pellets for analyses within the first 3 h from capture. All faecal samples were collected from the paper towels into plastic Eppendorf tubes (1.5 ml) using tweezers and stored at − 20 °C. Pellets clearly contaminated with urine (e.g. lying in urine spots) were not collected. Tweezers were cleaned with 70% alcohol after each sampling.

Analysis of faecal corticosterone metabolites

Extraction of steroids was conducted according to the method described by Palme et al. (2013). Briefly, each faecal sample was homogenised with mortar and pestle and an aliquot of 0.05 g was mixed with 80% methanol (1 ml) and shaken in a multi-vortex. We completed the extraction only when the sample mass was sufficient to provide a 0.05 g aliquot (e.g. Millspaugh and Washburn 2004; Blondel et al. 2016). The suspension was then centrifuged for 10 min at 2500 G. An aliquot of the supernatant was diluted (1:10) with assay buffer (Tris/HCl 20 mM, pH 7.5) and stored at − 20 °C until analysis.

To determine the amount of corticosterone metabolites, we used a 5α-pregnane-3β,11β,21-triol-20-one enzyme immunoassay (EIA). This EIA utilises a group-specific antibody measuring steroids with a 5α-3β,11β-diol structure. A detailed description of the procedures is given in Touma et al. (2003). The intra- and inter-assay coefficients of variation were 9.3 and 13.6%, respectively ($N = 9$ plates). The samples were grouped so that all the samples from one individual were on the same plate, and each plate had a similar number of samples coming from voles with different cognitive and behavioural profiles. The person doing the grouping of the samples was not the same that ran the EIA analysis. This part of the analysis was performed blind to the cognitive and behavioural profiles of the voles from which the samples were collected. The EIA has recently been validated for bank voles (Sipari et al. 2017).

Statistical analyses

Data were normalised through square-root transformation and analysed with R, version 3.2.3 (R Core Team 2015). We removed from the dataset two outliers that had indoor and open field values > 3 standard deviations higher than the means. We tested whether individual FCM levels were repeatable, i.e. consistent across contexts, using the 'rtpR' package and adjusting for treatment (Nakagawa and Schielzeth 2010; Stoffel et al. 2017). Repeatability is the proportion of phenotypic variation that can be attributed to between-individual variation (Nakagawa and Schielzeth 2010; Dingemanse and Dochtermann 2013). Adjusted repeatabilities are repeatabilities that control (adjust) for fixed effects (Stoffel et al. 2017) and describe the repeatability once the effect of the treatment has been removed, such that repeatabilities are calculated as if all measures were taken in the same conditions. We used restricted maximum-likelihood linear mixed models to evaluate the relationship between the FCM levels in each treatment and the behavioural and cognitive variables (activity, boldness, learning and reversal learning scores), considered as fixed effects. We ran separate models for each variable. In all models, sex, age and weight were added as fixed effects. The EIA plate and the litter identity were added as random factors in each model, specified as random intercept to control for inter-assay variation and to check for the possible effect of having siblings (maximum of four per litter) in our sample (e.g. Macrì and Würbel 2006; Rödel et al. 2010). We stepwise compared nested models with both random factors with simpler models. When a simpler model had a better fit (indicated by $2 \geq \text{AIC}_{\text{full}}–\text{AIC}_{\text{constrained}}$, where AIC is the Akaike information criterion) the second random factor was dropped (Zuur et al. 2009). We included all possible two-way interactions between the explanatory variables and excluded them stepwise if they were non-significant based on log-likelihood ratio tests (Zuur et al. 2009). We used the R packages nlme, version 3.1-131, and lme4, version 1.1-12 (Bates et al. 2015; Pinheiro et al. 2017). Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality.

We tested for phenotypic correlations between the physiological response to a change in environmental conditions (i.e., delta FCM, outdoor minus indoor FCM levels) and behavioural and cognitive variables using Spearman rank correlation tests. We could not run multivariate mixed models (MCMCglmm) to estimate covariances and correlations between traits due to the heterogeneity in place and time of the sampling. Given the different time of day at which the samples were collected, a similar comparison could not be made for the open field FCM levels because the corticosterone levels increase naturally during the day (Sipari et al. 2017). Since we selected extreme fast/inflexible and slow/flexible voles for the outdoor experiment, we also compared the difference in FCM levels of voles in indoor and outdoor conditions (outdoor - indoor) between these two groups with a Mann-Whitney *U* test to assess whether the two groups responded differently to the change in holding conditions. The accepted significance level was ≤ 0.05 throughout.

Results

At the population level, mean (± SD) concentrations of faecal corticosterone metabolites (FCMs) were 42.7 ± 23.9 ng/50 mg in indoor holding conditions, 38.3 ± 23.5 ng/50 mg in the outdoor holding conditions and 66.4 ± 48.8 ng/50 mg after the open field test. FCM levels did not differ between indoor and outdoor condition. Given the different time of day at which samples were collected, FCM levels could not be compared between open field test and the other two conditions. FCM levels were repeatable across contexts ($R_{\text{adj}} = 0.25$, 95% CI = 0.08–0.43, $P = 0.004$; unadjusted $R = 0.21$, CI = 0.04–0.38, $P = 0.008$), indicating that the rank order differences between individuals are maintained (Dingemanse and Wolf 2010). Both activity in the open field ($R = 0.74$, CI = 0.65–0.84, $P < 0.001$) and boldness towards a novel object ($R = 0.67$, CI = 0.68–0.89, $P < 0.001$) were repeatable over time. Bolder and less flexible individuals had lower FCM levels than shyer, more flexible individuals both in indoor and outdoor holding conditions (Table 1; Fig. 1). Activity and initial learning score were not related to FCM levels in any condition (Table 1). FCM levels after the open field were unrelated to any measured behavioural or cognitive variable (Table 1). The difference between FCM levels in holding conditions (outdoor-indoor) correlated negatively with boldness ($R_s = -0.48$, $P = 0.002$; Fig. 2a) and reversal learning scores ($R_s = -0.33$, $P = 0.04$; Fig. 2b). Reactive and proactive bank voles differed in their FCM level change between conditions (outdoor-indoor), with proactive voles having a lower Δ than reactive ones (Mann-Whitney U test: $W = 116$, $P = 0.02$, Fig. 3).

Discussion

Bank voles showed consistent differences between individuals in their physiological response to three different experimental conditions. We could detect relationships between FCM levels, boldness and flexibility (measured in reversal learning) but only in indoor and outdoor conditions. Individuals showing different personality and cognitive profiles were also shown to respond differently to the change from indoor to outdoor conditions, with proactive voles having lower FCM levels in the enclosures than in the cages, and reactive ones showing an opposite pattern. However, contrary to our expectations, all measured traits were independent from the HPA axis response induced by the open field test. Overall, our results provide only partial support for phenotypic correlation between behavioural, cognitive and HPA profiles predicted by the initial coping styles model.

According to our first prediction, individual FCMs were moderately repeatable across three different environmental conditions. These results are in line both with the assumptions of the coping style model and with previous studies conducted on bank voles (Eccard et al. 2011) and other vertebrates (reviewed in Taff et al. 2018). This is also the case for the study by Ferrari et al. (2013), which found repeatable within-individual consistency in physiological profiles in a

Table 1 Faecal corticosterone metabolites (ng/50 mg of dry faeces) in relation to activity, boldness, learning, reversal learning, age, sex, body mass and treatment of bank voles (*Myodes glareolus*) in indoor cages, outdoor enclosures and open field test. Statistically significant effects are highlighted in bold. Reference levels for categorical predictors are given in ()

	Indoor ($N = 70$)				Outdoor ($N = 40$)				Open Field ($N = 67$)			
Variable	Estimate	SE	F	P	Estimate	SE	F	P	Estimate	SE	F	P
Boldness												
Intercept	5.88	1.83	960.4	< 0.001	8.77	2.49	181.6	< 0.001	2.81	2.84	592.7	< 0.001
Boldness	− 0.58	0.22	9.4	**0.003**	− 1.04	0.21	23.2	**< 0.001**	0.34	0.33	0.2	0.689
Age	− 0.004	0.03	0.3	0.616	− 0.04	0.02	2.1	0.15	0.08	0.05	1.1	0.293
Sex (M)	1.19	0.62	8.6	**0.005**	0.46	0.73	0.2	0.66	2.35	0.96	16.1	**< 0.001**
Body mass	0.001	0.07	0.0003	0.985	− 0.05	0.08	0.3	0.56	0.03	0.11	0.1	0.775
Activity												
Intercept	6.08	1.98	889.4	< 0.001	7.01	2.97	211.7	< 0.001	2.32	2.97	589.1	< 0.001
Activity	− 0.32	0.23	2.8	0.100	− 0.45	0.26	3.3	0.081	0.30	0.34	0.02	0.901
Age	− 0.002	0.03	0.2	0.678	− 0.02	0.03	0.5	0.502	0.08	0.05	1.1	0.303
Sex (M)	1.40	0.64	9.0	**0.004**	0.65	0.83	0.6	0.448	2.20	0.95	15.7	**< 0.001**
Body mass	− 0.02	0.07	0.1	0.794	− 0.02	0.10	0.04	0.834	0.05	0.11	0.2	0.635
Learning												
Intercept	5.00	1.98	867.1	< 0.001	5.38	3.10	178.4	< 0.001	4.27	2.95	579.9	< 0.001
Learning	0.03	0.06	1.0	0.324	0.13	0.07	4.0	0.054	− 0.12	0.09	0.2	0.669
Age	0.01	0.03	0.1	0.819	− 0.03	0.03	1.0	0.331	0.08	0.05	1.2	0.275
Sex (M)	1.36	0.65	9.1	**0.004**	0.50	0.84	0.3	0.599	2.30	0.95	16.1	**< 0.001**
Body mass	− 0.01	0.07	0.0	0.912	− 0.03	0.10	0.1	0.800	0.05	0.11	0.2	0.668
Reversal learning												
Intercept	7.27	2.18	906.6	< 0.001	12.31	3.08	154.8	< 0.001	0.98	3.23	599.4	< 0.001
Reversal learning	− 0.11	0.06	4.3	**0.043**	− 0.23	0.07	10.7	**0.003**	0.12	0.09	1.0	0.325
Age	0.01	0.03	0.0	0.923	− 0.03	0.03	1.0	0.332	0.07	0.05	1.1	0.305
Sex (M)	1.32	0.63	9.3	**0.004**	0.80	0.81	0.6	0.464	2.30	0.95	16.2	**< 0.001**
Body mass	− 0.01	0.07	0.0	0.936	− 0.07	0.09	0.6	0.450	0.04	0.11	0.1	0.738

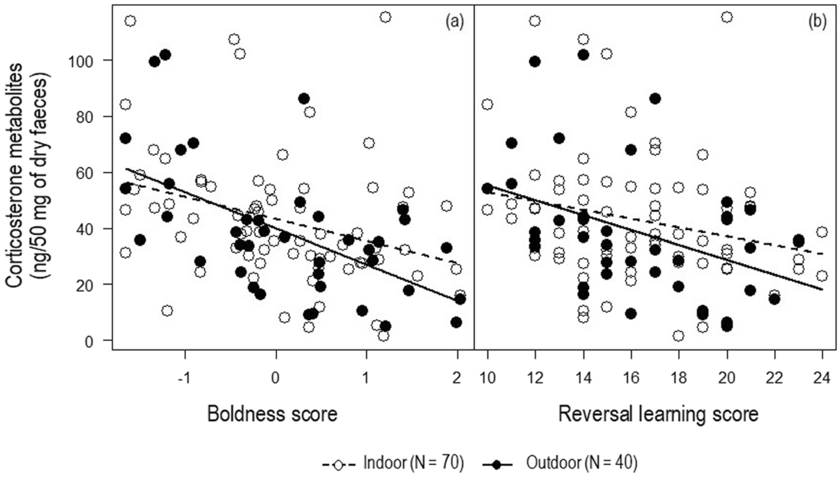

Fig. 1 Faecal corticosterone metabolites (ng/50 mg of dry faeces) of bank voles (*Myodes glareolus*) in relation to boldness (**a**) and reversal learning scores (**b**) in indoor (white symbols) and outdoor (black symbols) holding conditions. Represented are effects obtained from LMs (R^2: 0.19 (**a**); R^2: 0.15 (**b**)) for visual representation and raw data of individuals (dots)

natural population of marmots (*Marmota marmota*), even after years. In our study, we assessed the corticosterone secretion of the voles within hours (open field and cage conditions), and 2–4 months afterwards, which can be considered a long interval in the case of a short-lived small mammal (e.g. Bujalska 1975; Boratyński and Koteja 2009).

However, our prediction regarding the correlation of endocrine, behavioural and cognitive traits was only partially supported. We found some, but not all, of the correlations we expected between behavioural and cognitive traits and HPA axis activity and reactivity in different conditions. Proactive individuals (bolder, faster to learn but slower to reverse) showed indeed lower FCM levels compared with reactive individuals (shyer, slower to learn but flexible) when FCMs were measured when undisturbed in their indoor home cages and in outdoor enclosures. This supports the original coping style model, showing a direct connection between boldness and flexibility and HPA axis activity. However, there was no link between FCM levels and the behavioural and cognitive variables in the open field test. The original coping style model, predicts both lower HPA activity and reactivity to stressful challenges, therefore our results provide only partial support. Furthermore, we found no relation between activity and FCM levels in any condition. Previous studies, conducted both in laboratory and semi-natural conditions, offer mixed findings on this issue. Whereas several studies demonstrated correlations between various personality traits and responses to an acute stressor (e.g. Korte et al. 1992; Carere et al. 2003; Kralj-Fišer et al. 2007), others found that individuals with proactive personality traits had the highest HPA response to a stressor (e.g. Martins et al. 2007; Boulton et al. 2015), suggesting a non-linear connection between coping styles and HPA axis activity and reactivity (Koolhaas et al. 2010). Moreover, van Reenen et al. (2005) found no correlation between Holstein Friesian heifer calves' (*Bos taurus*) glucocorticoid levels and activity. Similarly, Westrick et al. (2019) found no correlation among FCMs and three behavioural measures of coping styles (activity, aggression and docility) in North American red squirrels (*Tamiasciurus hudsonicus*). Bebus et al. (2016) found no connection between corticosterone levels at the time of testing, learning and reversal learning in Florida scrub-jays (*Aphelocoma coerulescens*), although corticosterone levels during development predicted the cognitive performance. Similarly, Ferrari et al. (2013) showed that cortisol production under restraint was totally independent of other types of reactions to a stressor, both behaviourally and physiologically

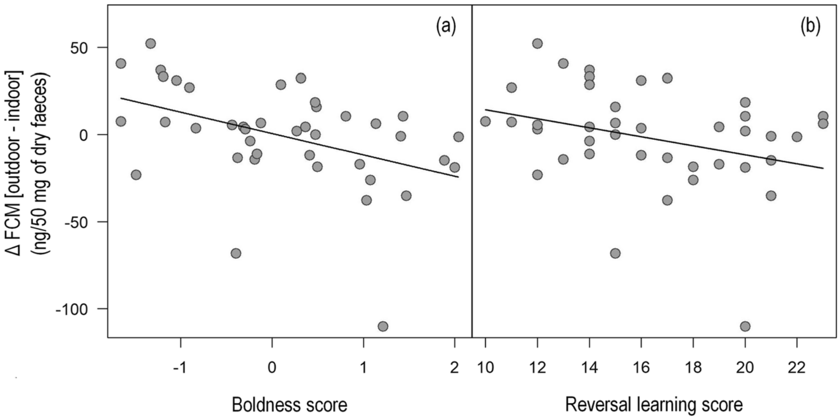

Fig. 2 Changes in concentrations of faecal corticosterone metabolites (ng/50 mg of dry faeces) between outdoor and indoor holding conditions (outdoor-indoor) in relation to boldness (**a**) and reversal learning scores (**b**). Represented are effects obtained from LMs (R^2: 0.18 (**a**); R^2: 0.13 (**b**)) for visual representation and raw data of individuals (dots)

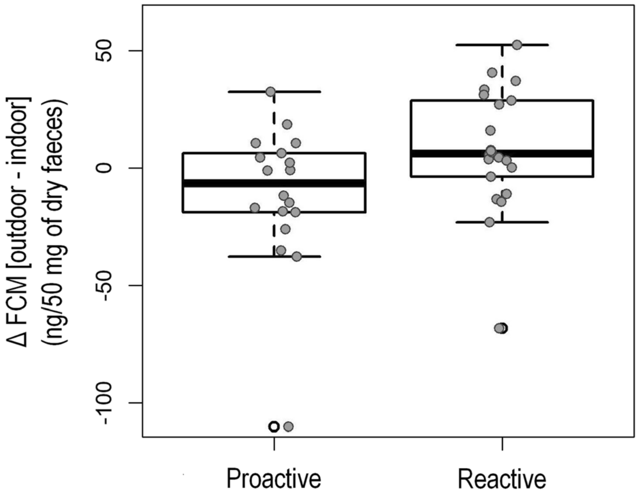

Fig. 3 Changes in concentrations of faecal corticosterone metabolites (ng/50 mg of dry faeces) between outdoor and indoor holding conditions (outdoor-indoor) for proactive (N = 18) and reactive (N = 22) bank voles (*Myodes glareolus*). Horizontal lines within box plots represent median values, boxes represent the interquartile range, and whiskers represent the range of values within 1.5 times the interquartile range. Individual data points are jittered

(e.g. locomotion, heart and breathing rate). Based on these and other findings, some authors have suggested that there might be at least two independent components of the stress response: the quantitative component (stress response) that describes the physiological aspects of the glucocorticoid production, and the qualitative component (coping style) comprises the behavioural and cognitive strategies employed in coping with the stressor (e.g. van Reenen et al. 2005; Koolhaas et al. 2010; Qu et al. 2018; Westrick et al. 2019). Thus, individuals showing similar behavioural responses (e.g. activity) may produce very different levels of glucocorticoids (van Reenen et al. 2005; Westrick et al. 2019). Our results regarding the HPA axis reactivity to challenges seem more in line with this two-tier model. Thus, further studies are needed to conceptually refine the coping style model and to investigate the relationship between behavioural, cognitive and endocrine profiles in more detail.

An alternative explanation for these mixed findings could be that the predictions made based on results obtained with selection lines might not hold for natural or non-selected populations. Similar to previous studies in wild, free-roaming or unselected populations (e.g. Dingemanse et al. 2004; Found and St Clair 2016; Bonnot et al. 2018; Zidar et al. 2019), the behavioural and cognitive traits we measured were distributed along a continuous proactive-reactive gradient. It is also worth noting that the more robust results in the present study refer to the outdoor condition. The voles assessed for their response to the new environment were chosen among those showing the more extreme proactive and reactive behavioural and cognitive traits. The responses of the individuals with intermediate behavioural and cognitive profiles might therefore have clouded the results for indoor holding condition and open field trials. If this is the case, future research would have to focus more on natural, unselected populations, preferably employing the natural stressors the animals experience in the wild (e.g. using predator cues or simulating predator attacks). Interpretation of findings and insights into apparently mixed results will also benefit from the investigation of responses to challenges presenting varying levels of complexity.

All animals in this experiment were born and raised in captivity and experienced semi-natural condition for the first time during the enclosure trials. This could have resulted in either an increase in the FCM levels due to the challenge of adjusting to a novel environment (e.g. Teixeira et al. 2007; Dickens et al. 2010; Parker et al. 2012) or in a decrease of FCM levels due to not being confined in a cage (e.g. Cooperman et al. 2004; Davis and Maerz 2011; Blondel et al. 2016). However, the direction of the change in FCM levels differed between proactive and reactive individuals. Proactive individuals' FCMs decreased or remained stable when moved outdoor, whereas reactive individuals' FCM levels mostly increased. Previous studies have found that after a period of adjustment and habituation, individuals show consistent and significant lower stress levels when kept in more natural conditions compared with cages (e.g. Schumann et al. 2014; Blondel et al. 2016). This has important consequences for animal welfare as well as for the reliability of behavioural and cognitive studies conducted with caged animals (e.g. Schumann et al. 2014; Blondel et al. 2016). One possible explanation for our results might be that individuals with different coping styles need different amounts of time to adjust to a new environment (e.g. Lowry et al. 2013; Sol et al. 2013). Proactive individuals are bolder, more active animals, relatively insensible to change, they explore a new environment faster (albeit superficially) and quickly form coping routines (e.g. Koolhaas et al. 1999, 2010; Sih and Del Giudice 2012). They might therefore have responded to the change of housing conditions with a lower corticosterone production to begin with, and took less time to adjust to more natural conditions. Reactive individuals, highly sensitive to environmental changes and slower in gathering information (e.g. Koolhaas et al. 1999, 2010; Sih and Del Giudice 2012), might have reacted more strongly to the change and have been retrieved from the enclosures while they were still in the process of adjusting (e.g. Schumann et al. 2014; Blondel et al. 2016). This is a rather speculative suggestion, although other observations imply that reactive individuals went through a change in their foraging behaviour, concentrating effort to the more protected areas and showing a significantly higher proportion of vigilance behaviour compared with proactive ones (Mazza et al. 2019). Further studies should investigate whether the change from cages to natural conditions affects proactive and reactive individuals differently and whether this is only a matter of habituation time.

Conclusions

HPA axis activity proved to be a repeatable trait in bank voles and correlated with some personality traits, at least under some conditions. HPA axis response to induced stress, however, did not correlate with any other trait and our results might therefore be better explained by the updated coping styles model involving two different and separate axes (Koolhaas et al. 2010). Determining whether or not this two-tier model is generally true across species and/or environmental contexts will require further studies, more attention to natural populations, and wider adoption of repeated measures designs to allow within- and among-individual sources of co-variation to be disentangled.

This study also highlights that experiments conducted in what are supposed to be controlled and protected conditions, might reveal patterns that are not consistent with natural conditions and that the sole fact of being confined might differentially affect individuals and their responses to stressors and other environmental effects.

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Data availability Data are available as supplementary material

Compliance with ethical standards

Competing interests The authors declare that they have no competing interests.

Ethical approval Ethical approval for involving animals in this study was given by the "Landesamt für Umwelt, Gesundheit und Verbraucherschutz Brandenburg" (reference number: V3-2347-44-2011, Ä6) and the "Landesamt für Natur, Umwelt und Verbraucherschutz Nordrhein-Westfalen" (reference number: 84-02.04.2016.A253) as well as by the ethical committees of the institutions where the study took place. This study complies with the ASAB/ABS Guidelines for the Use of Animals in Research and was conducted in accordance with all applicable international, national and institutional guidelines for the care and use of animals.

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