Personality tips the scale: How individual differences in exploration shape behavioural and hormonal adjustment to different environments

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Abstract

Individuals show consistent differences in their behaviour across time and/or context, usually referred to as animal personality in behavioural ecology. These inter-individual differences raised the question if animals of different personalities also vary in how they adjust to certain environmental conditions. In the present study, we aimed to investigate personality-dependent adjustments to different environmental conditions. By means of two distinct experiments, rats were characterised regarding their level of exploration and exposed to an environment with a predictable versus an unpredictable food availability (experiment 1) or to an environment with a social partner of matching versus mismatching personality (experiment 2). To assess behavioural differences between individuals of varying exploration levels, the home cage behaviour of the animals was monitored and two tests for measuring anxiety-like behaviour were conducted. Furthermore, concentrations of basal faecal corticosterone metabolites were determined to record hypothalamic–pituitary–adrenocortical activity repeatedly. The characterisation showed consistent inter-individual differences in exploration levels in both experiments. While personality, environment and the interaction of both did not affect basal faecal corticosterone metabolite concentrations in neither of the experiments, several behavioural differences between individuals of varying exploration levels were detected in the home cage and in the tests. Most interestingly, interactions between personality and environment were found, pointing towards a better behavioural adjustment of highly explorative animals to predictable conditions. Therefore, the results emphasise the existence of context-specific personality-dependent behavioural adjustment. Moreover, personality-dependent differences in affiliative behaviour and environment-dependent differences in welfare-associated measures were reported, highlighting the importance of integrating personality into both eco-evolutionary perspectives on adjustment processes and animal welfare endeavours.

Introduction

Individuals show consistent differences in their behaviour across time and/or context, usually referred to as animal personality in behavioural ecology (Kaiser & Müller, 2021; Stamps & Groothuis, 2010). Thereby, an animal’s personality has been described as a composition of different personality traits, such as “boldness” or “aggressiveness”, that can be reflected by multiple behaviours (Kaiser & Müller, 2021). Over the past years, evidence for these consistent inter-individual differences has been documented for many different taxa, from primates to insects (Gosling, 2001), basing observations on a variety of different measurements. Among these, there are behavioural parameters, such as exploration and vocalisation (Mällo et al., 2007; Réale et al., 2007), but meanwhile the animal personality framework even expands towards endocrinological parameters, such as glucocorticoid levels (Fanson & Biro, 2019; Taff et al., 2018).

Interestingly, such findings on consistent personality traits challenge the idea that variation between individuals is centred around an evolutionary optimum shaped by natural selection (Dall et al., 2004; Sih et al., 2004). Thus, the question arises as to how animal personalities could have evolved and how they are maintained within a population (Sih et al., 2004). In fact, several hypotheses exist in this regard (e.g. reviewed in Bergmüller & Taborsky, 2010; Wolf & Weissing, 2010, 2012), one of them suggesting that consistent personality traits are favoured, as constant adaptation to changeable conditions might be too costly. This would allow appropriate responses on an average level, leading to similar fitness effects for each of the different personalities (Wolf & Weissing, 2010). At the same time, this trade-off is likely to come along with limited coping abilities under specific environmental conditions (Sih et al., 2004), raising the question of how such constraints translate into fitness consequences. In this context, Smith and Blumstein (2008) published a meta-analysis on fitness consequences and survival of different personality traits, revealing exploration to have positive effects on survival. More recent studies suggest, however, that this effect might be dependent on the specific context or the environmental condition the animals experience (Brehm & Mortelliti, 2024; Haage et al., 2017).

For instance, proactive animals, i.e. more bold, active and aggressive individuals with a lower hypothalamic–pituitary–adrenocortical (HPA) axis (re-)activity and less cognitive flexibility (Koolhaas et al., 1999; Mazza et al., 2018), seem to perform better under stable environmental conditions, while reactive animals, i.e. less bold, active and aggressive individuals with a higher HPA axis (re-)activity and greater cognitive flexibility (Koolhaas et al., 1999; Mazza et al., 2018), seem to adjust better to changing environments (Benus et al., 1991; Verbeek et al., 1994). Based on these studies, several other studies systematically investigated personality-dependent variation in environmental adjustment, for instance, to different foraging conditions. Indeed, depending on the individuals' personality, differences occurred regarding the use of space and food resources as well as concerning risk taking behaviour (Mazza, Jacob, et al., 2019; Wauters et al., 2021; Wirowska et al., 2024). Likewise, personality-dependent adjustment to an individual's social environment is documented (reviewed in Mittelbach et al., 2014; Webster & Ward, 2011). In fish, for instance, it has been found that shy personality types show a more pronounced adjustment to their social environment, which is expressed in greater behavioural changes compared to bold individuals (Magnhagen & Staffan, 2005). More specifically, shy individuals became even more shy in the presence of bold conspecifics, highlighting the impact of the partner animal's personality as a factor of the individual's social environment. In line with this, a study in primates documents that the interplay between an individual's personality and the personality of group members affects behavioural outcomes. In fact, individuals with more similar personality types were more likely to form close social bonds, supporting the principle of homophily (Massen & Koski, 2014).

Taken together, these findings suggest that the interaction between an individual's personality and its environment can be a key determinant of behavioural and physiological outcomes. In the present study, we therefore aimed to systematically investigate such personality-dependent adjustments to different environmental conditions. More specifically, we repeatedly tested the animals in the Open field to assess consistent individual differences in their exploratory locomotion, referred to as "trait exploration" in the following. Subsequently to the characterisation, the animals were assigned to different environmental conditions: In experiment 1, individuals were confronted with an environment characterised by either a predictable or an unpredictable food availability. In experiment 2, individuals were housed with a social partner of either a matching or mismatching personality. While most studies investigating effects of social factors have focussed on group-level parameters such as group size and composition (e.g. Olsson & Westlund, 2007), we here examine the effects of the social partner's personality, a social factor on the individual level that has been mainly overlooked so far. To assess behavioural differences, we monitored the home cage behaviour of the animals and conducted two tests for anxiety-like behaviour. Furthermore, we repeatedly determined faecal corticosterone metabolites (FCMs) to assess HPA axis activity (Palme, 2019). In line with the literature, we hypothesised individuals to display repeatable individual differences in exploratory locomotion. In addition, we hypothesised that trait exploration interacts with the respective environmental condition in such a way that individuals differ in their behavioural and endocrinological responses depending on both their personality and the environment they live in.

Animals, materials & methods

Animals and housing conditions

The study consisted of two experiments, each including 24 female Lister Black Hooded rats, ordered at postnatal day (PND) 28 from Charles River Laboratories (Research Models Services, Germany GmbH, Sulzfeld, Germany). The rats were delivered in three batches per experiment, with 8 females per batch and all animals could be identified by their individual fur pattern. Animals of each batch were housed in same-sex groups of 8 individuals until PND 86±1 and in groups of 4 (experiment 1) or groups of 2 (experiment 2) for the remaining duration of the experiment (Fig. 1). The cages (Furat, Ferplast, Italy; 48 cm x 78 cm and 70 cm high) contained wood shavings as bedding material (TierWohl Super, J. Rettenmaier and Söhne GmbH & Co KG, Rosenberg, Germany), two additional floors, paper tissues as nesting material, four wooden cubes, a cardboard tunnel, two hanging houses (Sputnik, SAVIC, Belgium; 29 cm x 26 cm and 19 cm high), a semi-transparent red plastic house (ZOONLAB GmbH Animal Husbandry Experts, Germany; 20.5 cm x 15.7 cm and 11.5 cm high) and a semi-transparent red plastic tunnel (ZOONLAB GmbH Animal Husbandry Experts, Germany; 15 cm x 9 cm and 9.5 cm high). Thereby, the housing conditions exceeded the standard housing conditions for laboratory rats regarding floor space (approximately two times a standard Makrolon Typ IV cage) and number of enrichment items. In experiment 1, water was offered *ad libitum*, while food (Dustless Precision Pellets, Grain-Based, 45 mg, Bio-Serv, New Jersey, United States) was offered *ad libitum* until PND 90 and limited thereafter until the end of the experiment (for details see below). In experiment 2, water and food (Altromin 1324, Altromin Spezialfutter GmbH & Co. KG, Lage, Germany) were offered *ad libitum* at all times. Each experiment was carried out in a separate housing room that was maintained at a reversed dark/light cycle with lights off at 9 am, a temperature of ~22 °C, and a relative humidity of about 50%.

Experimental design

Both experiments consisted of a characterisation and a subsequent exposure phase, where the rats were distributed to different environmental conditions (experiment 1: predictable versus unpredictable food availability, experiment 2: matched versus mismatched social partner; Fig. 1). In the characterisation phase, rats were tested for their exploratory locomotion in the Open field (OF) in order to assess trait exploration. The test was repeated three times (PND 70, 77 and 84), as this was found to deliver robust results regarding temporal consistency (Martin et al., 2011). Subsequently to the characterisation phase, faecal corticosterone metabolites (FCMs) were determined (PND 85) and the animals were distributed to the different environmental conditions under which they were housed for approximately four weeks (PND 86±1 - 114±1). Within this exposure phase, the home cage behaviour (HCB) was monitored (PND 90-108), faecal samples for FCM analysis were collected two more times (PND 91 & 108) and two behavioural tests for anxiety-like behaviour were conducted (Elevated plus maze (EPM): PND 111, Free exploration test (FET): PND 112-114±1) (for details regarding the different test procedures see below). At all times, rats were exclusively cup-handled from their arrival until the end of the experiment.

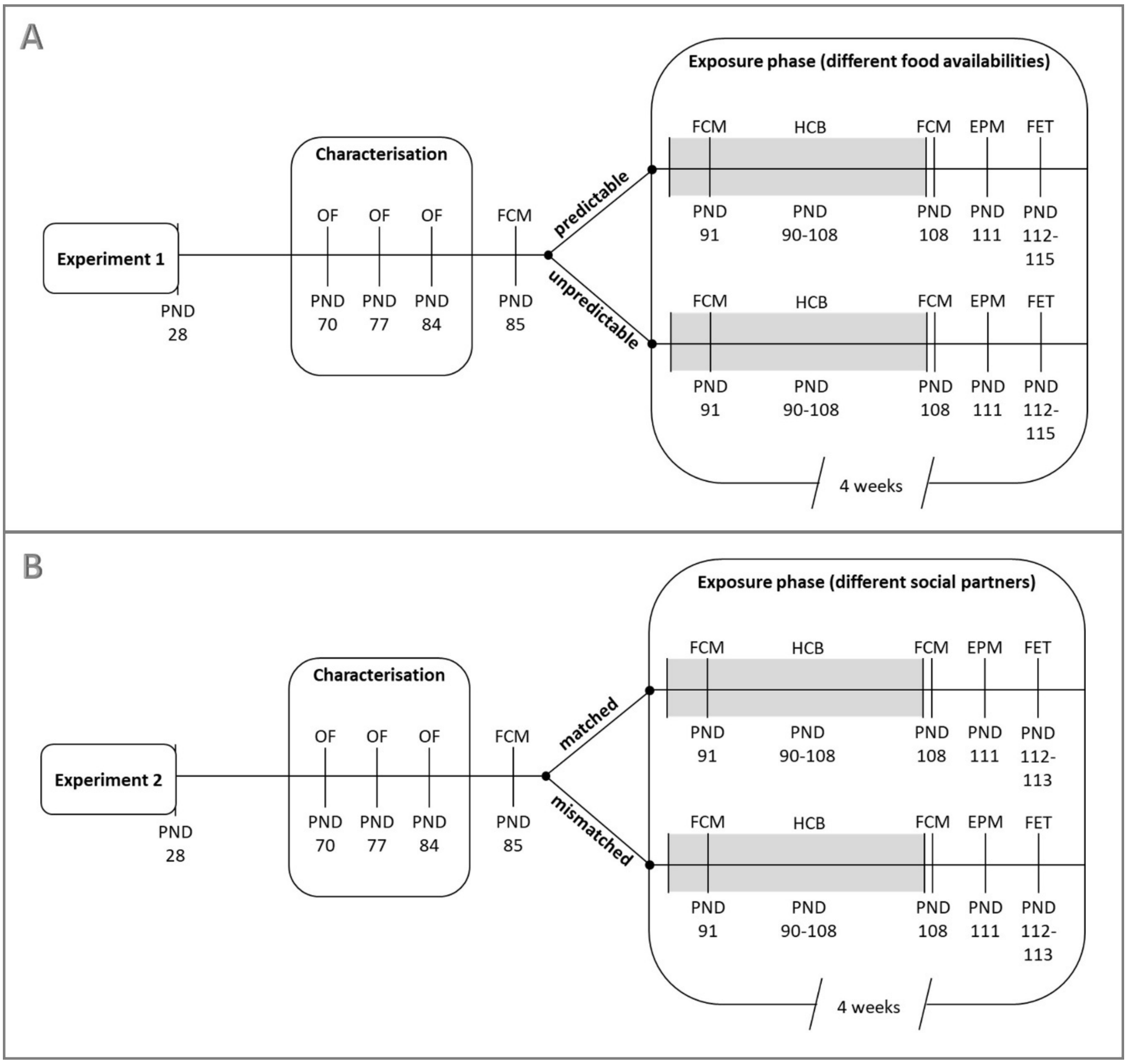

Figure 1: Experimental design of experiment 1 (A) and 2 (B). After the rats were characterised by repeatedly testing them in the Open field (OF; PND 70, 77 and 84), faecal corticosterone metabolites (FCM) were collected (PND 85). Subsequently, the animals were distributed to the different environmental conditions (Experiment 1: predictable versus unpredictable food availability, experiment 2: matched versus mismatched social partner) and housed under these conditions for four weeks (PND 86±1 - 114±1). Within this phase the home cage behaviour (HCB) was monitored (PND 90-108), faecal corticosterone metabolites (FCM) were collected twice (PND 91 & 108) and two behavioural tests for anxiety-like behaviour were conducted (Elevated plus maze (EPM): PND 111, Free exploration test (FET): PND 112-114±1).

Experiment 1: predictable versus unpredictable food availability

Experiment 1 was designed to concentrate on personality-dependent adjustment to a non-social environmental factor, i.e. the food availability, which was either predictable or unpredictable. Regarding this factor, variation in adjustment depending on an individuals' personality is assumed and has already been reported in previous studies (Mazza, Jacob, et al., 2019; Réale et al., 2007; Wauters et al., 2021; Wirowska et al., 2024). After the characterisation phase, rats were ordered from high to low trait exploration and then distributed to the two environments in an alternating order, for which the first assignment was pseudorandomised across batches. For example, if the rat with the highest trait exploration in the first batch was assigned to the predictable food availability environment, the rat with the second highest trait exploration was assigned to the unpredictable environment, and so on until all animals were allocated. In the following batch, the assignment order was reversed, such that the rat with the highest trait exploration was placed in the unpredictable environment and the rat with the second highest trait exploration in the predictable one. This procedure ensured that trait exploration was balanced across environments.

The differences in food availability were created by using automated feeders (Pellet Dispenser with IR Sentry, 45 mg, pedestal mount, OCB Systems Ltd, Sawbridgeworth, United Kingdom). In the predictable condition, the feeders were programmed to deliver 37 pellets (Dustless Precision Pellets, Grain-Based, 45 mg, Bio-Serv, New Jersey, United States) every 20 minutes for 12 hours starting at 9 am, while in the unpredictable condition the sum of pellets for the day was the same (1332 pellets between 9 am and 9 pm), but time and amount of food delivery were randomised within the 12 hours interval. Nevertheless, an interval with no food delivery did never exceed 24 hours. The total amount of food, i.e. ~60 g, was calculated based on a pilot project prior to the experiment. The feeders were attached to the cage and delivered the food pellets via a tube into the food bowl used before in the home cage of the rats. To ensure that each individual receives a sufficient amount of food (i.e. maintaining or increasing initial *ad libitum* weight) during the exposure phase, individuals' current percentage bodyweights were calculated by daily weighing in the morning (PCE-BT 2000, PCE Deutschland GmbH, Meschede, Germany; weighing capacity: 2100 g, resolution: 0.01 g). The calculation was based on the *ad libitum* bodyweights determined by daily weighing in the week before the rats were assigned to the different environmental conditions. Since all animals maintained or increased their bodyweight across the exposure phase, no additional feeding was required.

Experiment 2: matched versus mismatched social partner

Experiment 2 was designed to concentrate on personality-dependent adjustment to a social environmental factor, i.e. the social partner, which was either of matching or mismatching personality, as regarding this factor personality-dependent differences in adjustment are assumed and already reported (Magnhagen & Staffan, 2005; Massen & Koski, 2014; Oosten et al., 2010). After the characterisation phase, rats were ordered from high to low trait exploration and then distributed to the two environments in an alternating order, for which the first assignment was pseudorandomised across batches. However, whenever an animal was assigned to the matched condition the animal right next to it on the continuum was chosen as the social partner to create the best match possible based on the trait exploration continuum that was observed. For example, if the rat with the highest trait exploration in the first batch was assigned to the mismatched social partner environment, the rat with the second highest trait exploration was assigned to the matched social partner environment together with the rat with the third highest trait exploration. This was continued until all animals were allocated. In the following batch, the assignment order was reversed, such that the rat with the highest trait exploration was placed in the matched social partner environment together with the rat with the second highest trait exploration, while the rat with the third highest trait exploration was placed in the mismatched social partner environment. This procedure ensured that trait exploration was balanced across environments.

Characterisation phase

Open field (OF)

The OF is a behaviour test that is commonly used to evaluate anxiety-like behaviour and exploratory locomotion in rodents, which naturally tend to avoid open and bright areas (Archer, 1973; Treit & Fundytus, 1988). In the field of animal personality research, the OF has become one of the most widely used behaviour tests, repeatedly performed to assess activity, exploration and boldness as consistent personality traits (Améndola et al., 2022; Herde & Eccard, 2013; Mazza et al., 2018; Réale et al., 2007; Santicchia et al., 2022; Wirowska et al., 2024; Yuen et al., 2017). Moreover, a previous study working with rats of the same strain and age documented high repeatability estimates for the total distance travelled in the arena of the OF (Quante et al., 2025), supporting the use of this parameter for the characterisation in the present study. The OF apparatus consisted of a square grey plastic arena measuring 104 cm × 104 cm, with walls 40 cm high. To prevent rats from climbing or jumping onto the walls, transparent flexible plastic protectors were placed on top. The area within 26 cm of the walls was designated as the peripheral zone, while the central 52 cm × 52 cm section was defined as the centre zone. The arena was illuminated from above at an intensity of ~35 Lux.

The OF was conducted on PND 70, 77, and 84 between 9 am and 1 pm on each testing day. Rats were tested in a randomised order in a dedicated testing room and placed inside a semi-transparent red plastic box (22 cm × 22 cm × 15 cm), which was cleaned between individuals, for transportation. Prior to each test, rats remained inside the transport box for 1 minute to ensure that all animals were in the same state of arousal when being tested (Izídio et al., 2005). Afterwards, the rat was placed in the front left corner of the arena, facing the wall. The behaviour of the rat was recorded and automatically tracked by using a camera (Logitech HD Pro C920 Full HD-Webcam 1920 x 1080 Pixel, Logitech, Apples, Switzerland) and a tracking software (ANY-maze Video Tracking Software, version 6.32, Stoelting Co., Wood Dale, United States). The test duration was 5 min, and the experimenter left the room during testing to prevent bias. The apparatus was cleaned with 70% ethanol and paper towels before testing the first rat as well as between rats.

Exposure phase

Faecal corticosterone metabolites (FCM)

Faecal corticosterone metabolites (FCMs), which serve as a non-invasive indicator of pituitary-adrenocortical activity (Palme, 2019), were measured to assess the animals' baseline corticosterone levels before they were distributed to the different environments (PND 85), right after they entered the new environmental conditions (PND 91) and at the end of the exposure phase (PND 108). Sampling was conducted between 1 pm and 3 pm in the animals' housing room on all sampling dates. For a period of exactly 2 hours, rats were individually housed in prepared Makrolon Type IV cages containing a small amount of bedding, a paper tissue, a semi-transparent red plastic house, and provided with food and water *ad libitum*. Following the sampling period, rats were returned to their home cages, and faecal pellets were collected using gloves. All faeces from a given cage were transferred into a labelled 25 ml Eppendorf tube (Eppendorf AG, Hamburg, Germany) and stored at −27.5 °C until analysis.

For the analysis of FCMs, the wet weight of each faecal sample was first determined using a precision scale (Model 510-23, Kern, Balingen, Germany; weighing capacity: 300 g, resolution: 0.001 g). Samples were then dried in an oven (Model 500, D-06061, Memmert, Schwabach, Germany) at 80 °C for 3 hours. After drying, the samples were reweighed and stored in 25 ml Eppendorf tubes. The dried faeces were subsequently ground to a fine powder using a mixer mill (Mixer Mill MM 400, Retsch, Haan, Germany) equipped with a stainless-steel ball (diameter: 12–15 mm, Retsch, Haan, Germany). A 70 mg portion of the faecal powder was transferred into a 2 ml Eppendorf tube and mixed with 1.4 ml of 80% methanol. The mixture was vortexed for 30 minutes (Multi-vortex V-32, Kisker, Steinfurt, Germany) and then centrifuged at 5,200 rpm for 10 minutes (Centrifuge 5415 R, Eppendorf, Hamburg, Germany). From the resulting supernatant, 500 µl was collected and stored in a 2.0 ml safe-lock Eppendorf tube at −20 °C. FCM concentrations were subsequently measured using a 5α-pregnane-3β,11β,21-triol-20-one enzyme immunoassay (see Lepschy et al., 2007; Touma et al., 2003).

Home cage behaviour (HCB)

To monitor the animals' behaviour under the different environmental conditions, daily home cage behaviour observations were carried out during the exposure phase (PND 90-108). Observations took place 6 times a week, whereas 3 observation intervals were scheduled before noon and 3 observations in the afternoon. The home cage behaviour was assessed using focal continuous sampling for 5 minutes on each animal, with a pseudorandomised observation order in which two animals from the same cage were never observed directly after each other. In experiment 1, the experimenter was blinded to the individual's trait exploration and in experiment 2, the experimenter was blinded to the individual's trait exploration and the environmental condition. The recorded behaviours were grouped into the following main categories: *Inactivity*, *General activity*, *Affiliative behaviour*, *Agonistic behaviour*, *Maintenance behaviour*, *Abnormal behaviour* (for details see supplementary material).

Elevated plus maze (EPM)

The EPM is a widely used behaviour test for rodents, designed to assess anxiety-like behaviour based on the animals' natural avoidance of open and bright spaces (Lister, 1987; Pellow et al., 1985; Rodgers & Johnson, 1995; Treit et al., 1993). The apparatus consisted of a plus-shaped structure made of grey plastic, featuring two opposing closed arms (52 cm × 10 cm), two opposing open arms (52 cm × 10 cm), and a central square zone (10 cm × 10 cm). The closed arms were enclosed by 30 cm high walls, topped with transparent flexible plastic protectors to prevent the rats from jumping and walking on the walls. The open arms were bordered by a 0.4 cm edge to provide safety when rats would lean over. The entire maze was elevated 60 cm above the floor and consistently positioned in a fixed orientation within the testing room across all experimental sessions. The test apparatus was illuminated from above at an intensity of ~25 Lux.

In both experiments of the present study, the EPM was performed on PND 111 between 1 pm and 5 pm. Rats were tested in a randomised order in a dedicated testing room and placed inside a semi-transparent red plastic box (22 cm × 22 cm × 15 cm), which was cleaned between individuals, for transportation. Prior to each test, rats remained inside the transport box for 1 minute to ensure that all animals were in the same state of arousal when being tested (Izídio et al., 2005). Afterwards, the rat was put in the centre zone of the test apparatus, facing the open arm of the maze. The behaviour of the rat was recorded and automatically tracked by using a camera (Logitech HD Pro C920 Full HD-Webcam 1920 x 1080 Pixel, Logitech, Apples, Switzerland) and a tracking software (ANY-maze Video Tracking Software, version 6.32, Stoelting Co., Wood Dale, United States). The test duration was 5 min, and the experimenter left the room during testing to prevent bias. The apparatus was cleaned with 70% ethanol and paper towels before testing the first rat as well as between rats. Measured parameters were the relative entries and relative time spent on the open arms, the distance travelled on the open arms, the sum of entries into the open and closed arms and the total distance travelled (Rodgers & Johnson, 1995; Treit et al., 1993).

Free exploration test (FET)

The FET is a behaviour test that determines anxiety-like behaviour in rodents (Griebel et al., 1993). While being similar to the OF, it is less often used in behavioural ecology with the main difference being that the tested animal is not directly confronted with an unknown environment, but that it can freely chose if it wants to leave a familiar environment to explore, thereby covering another aspect of anxiety-like and exploratory behaviour. For the FET the home cage of the animal was connected to the OF arena (for details see above) with a tunnel (2 x Tunnel FPI 4844, Ferplast, Italy; length: 25 cm, diameter: 10.5 cm). The test arena was illuminated from above with a light intensity of ~35 Lux.

The FET was performed on PND 112-114±1 between 2 pm and 5 pm, with the rats being tested in a randomised order in a separate test room. As this test included the home cage of the tested individual, all other animals from the cage were temporarily put in a Makrolon Type IV cage equipped with bedding and *ad libitum* access to water for the duration of the test. To prevent an effect of this procedure on the test results, only one rat per cage was tested per day. For the transport of the animals to the test room a semi-transparent red plastic box (22 cm x 22 cm and 15 cm high) was used, which was cleaned between individuals. Before the start of the test, the rat spent 2 min inside the transport box for acclimatisation, to make sure that all animals were in the same state of arousal when being tested (Izídio et al., 2005). During that time the home cage of the animal was connected to the arena. Then, the rat was put back into its home cage. The behaviour of the rat inside the arena was recorded and automatically tracked by using a camera (Logitech HD Pro C920 Full HD-Webcam 1920 x 1080 Pixel, Logitech, Apples, Switzerland) and a tracking software (ANY-maze Video Tracking Software, version 6.32, Stoelting Co., Wood Dale, United States). The test duration was 15 min and during testing, the experimenter left the room to prevent bias. Before the first rat as well as between rats the apparatus and the tunnel were cleaned with 70% ethanol and paper tissues. Measured parameters were the latency to enter the arena, the entries made into the arena and the time spent there as well as the distance travelled inside the arena (Krakenberg et al., 2019).

Statistics & Sample sizes

The two experiments of the present study were planned with a sample size of 24 female rats each, based on an a priori power analysis performed in G*Power (version 3.1.9.7) that aimed to detect an average effect size (f = 0.3) with a power of 80%. In experiment 2, one individual was excluded from the study before testing started, two individuals were excluded at the end of the characterisation phase and one individual was excluded in the middle of the exposure phase, due to health issues that were not related to the experiment (for details see supplementary material). As this experiment is based on housing the animals in pairs, the cage partner had to be removed from the study as well. Thus, for experiment 2, this results in a sample size of 23 individuals for the characterisation phase, a sample size of 18 individuals for FCM and HCB and a sample size of 16 for the EPM and FET.

All analyses for both experiments were conducted in R version 4.4.0 (R Core Team) and significance levels of $0.05 < p \leq 0.1$ were considered a trend, while $p \leq 0.05$ was considered significant. Moreover, estimates whose 95% confidence intervals (CI) did not overlap zero were considered significant. To verify the temporal consistency of inter-individual differences in exploratory locomotion, we first determined a repeatability estimate (R) for the distance travelled in the OF. Repeatability estimates are often used in animal behaviour to quantify the consistency of individual differences (e.g. Bell et al., 2009; Nakagawa & Schielzeth, 2010). Using the rptR package in R, the repeatability was estimated in a univariate, linear mixed effects model framework (Stoffel et al., 2017). The model was fitted with the test repetition as a fixed effect and individual ID as a random effect. The uncertainty of the repeatability estimates, i.e. confidence intervals, was calculated using parametric bootstrapping (n = 1000, confidence level = 95%) and the statistical significance was tested by likelihood ratio tests.

To investigate effects of trait exploration, environmental condition and the interaction of both, (general) linear mixed models ((G)LMMs) were used ("lme4" package; Bates et al., 2015), with the interaction of trait exploration and environmental condition as fixed effects. Moreover, the timepoint was added as a fixed effect for the FCM model and the models on HCB. Concerning the HCB, data from each individual was pooled by week. Please note that for experiment 1 the HCB Bar mouthing was excluded from the analysis, due to its rare occurrence. In the models, "Batch" or "ID" were used as a random effect, depending on whether the data included repeated measures per individual. Please note, that for experiment 2 "Cage" was tested as a random effect as well by comparing the Akaike information criterion (AIC) (see Zuur et al., 2010) but was found to not improve model fit. Thus, the final models for FCM and HCB included the interaction of trait exploration and environmental condition, and also timepoint as fixed effects as well as ID as a random effect (FCM/HCB ~ trait exploration * environmental condition + timepoint + (1|ID), family = gaussian/poisson), while the final models for the EPM and FET included the interaction of trait exploration and environmental condition as fixed effects and Batch as a random effect (EPM/FET ~ trait exploration * environmental condition + (1|Batch), family = gaussian/poisson). For all models, "DHARMa" package (Hartig, 2024) was used to check model residuals and significance of fixed effects was assessed using likelihood ratio chi-square tests (Type III). If appropriate, the "emmeans" package ((Lenth, 2024); pairwise comparisons adjusted using

Tukey's method) was used to perform subsequent post hoc analyses. For Gaussian models (LMMs), denominator degrees of freedom were estimated using the Kenward–Roger approximation, yielding t-tests. For non-Gaussian models (GLMMs), asymptotic Wald tests were used, yielding z-tests.

Ethical Note

All procedures complied with the regulations covering animal experimentation within Germany (Animal Welfare Act) and the EU (European Communities Council DIRECTIVE 2010/63/EU) and were approved by the local (Gesundheits- und Veterinäramt Bielefeld, Nordrhein-Westfalen) and federal authorities (Landesamt für Verbraucherschutz und Ernährung "LAVE NRW" (formerly Landesamt für Natur, Umwelt und Verbraucherschutz Nordrhein-Westfalen "LANUV"), reference number: 81-02.04.2022.A101).

The welfare of the animals was carefully monitored during the whole experiment and beyond. Testing was conducted during the active phase of the animals only and was based solely on non-invasive methods. The housing conditions included spacious cages with multiple levels and a variety of enrichment items. After the experiment, rats remained in the housing facility, were rehomed or handed over to a cooperation partner.

Results

Experiment 1: predictable versus unpredictable food availability

Characterisation phase

The repeatability analysis for characterising the animals regarding their exploratory locomotion in the Open field (OF) revealed temporally consistent inter-individual differences (R = 0.370, CI: [0.100, 0.613], p = 0.001), indicating exploratory locomotion to be a consistent personality trait.

Exposure phase

Personality-by-environment interaction effects

The analysis of faecal corticosterone metabolites (FCMs) did not detect a significant interaction between trait exploration and food availability in experiment 1 ($\chi2 = 0.391$, df = 1, p = 0.531) (Fig. 2). Regarding home cage behaviour (HCB), a significant interaction effect of trait exploration x food availability was found for *Huddling* (χ2 = 7.335, df = 1, p = 0.007) (Fig. 3). Post hoc testing revealed that under a predictable food availability, individuals with a higher tendency to explore showed significantly longer huddling durations than individuals with a lower trait exploration (slope estimate = 0.555 ± 0.215, CI: [0.107, 1.004]). This association differed significantly from the one under an unpredictable food availability. Here, there was a negative relationship between trait exploration and huddling duration on a descriptive level (slope estimate = -0.307 ± 0.235, CI: [-0.796, 0.183]; slope comparison estimate = 0.862 ± 0.318, t = 2.708, p = 0.014), demonstrating personality-dependent behavioural adjustment to differences in food availability. Moreover, there was a trend for an effect of trait exploration x food availability for *Agonistic behaviour* (χ2 = 3.471, df = 1, p = 0.062; Fig. 3) and *Maintenance behaviour* (χ2 = 3.788, df = 1, p = 0.052). Specifically, individuals with a higher tendency to explore were characterised by decreasing agonistic (slope estimate = -0.101 ± 0.060, CI: [-0.220, 0.017]) and decreasing maintenance behaviour (slope estimate = -0.043 ± 0.272, CI: [-0.097, 0.010]) in predictable conditions. In both cases, this association showed a trend to differ from the relationship found in the unpredictable food availability condition, where agonistic and maintenance behaviour increased on a descriptive level for individuals with a higher tendency to explore (*Agonistic behaviour*: slope estimate = 0.048 ± 0.053, CI: [-0.055, 0.152], slope comparison estimate = -0.150 ± 0.080, z = -1.863, p = 0.063; *Maintenance behaviour*: slope estimate = 0.036 ± 0.030, CI: [-0.023, 0.095], slope comparison estimate = -0.079 ± 0.041, z = -1.946, p = 0.052). For the remaining behavioural parameters, i.e. *Inactivity*, *General activity*, *Affiliative behaviour* and *Foraging*, no significant interaction effects of trait exploration and food availability were detected (for details see supplementary material).

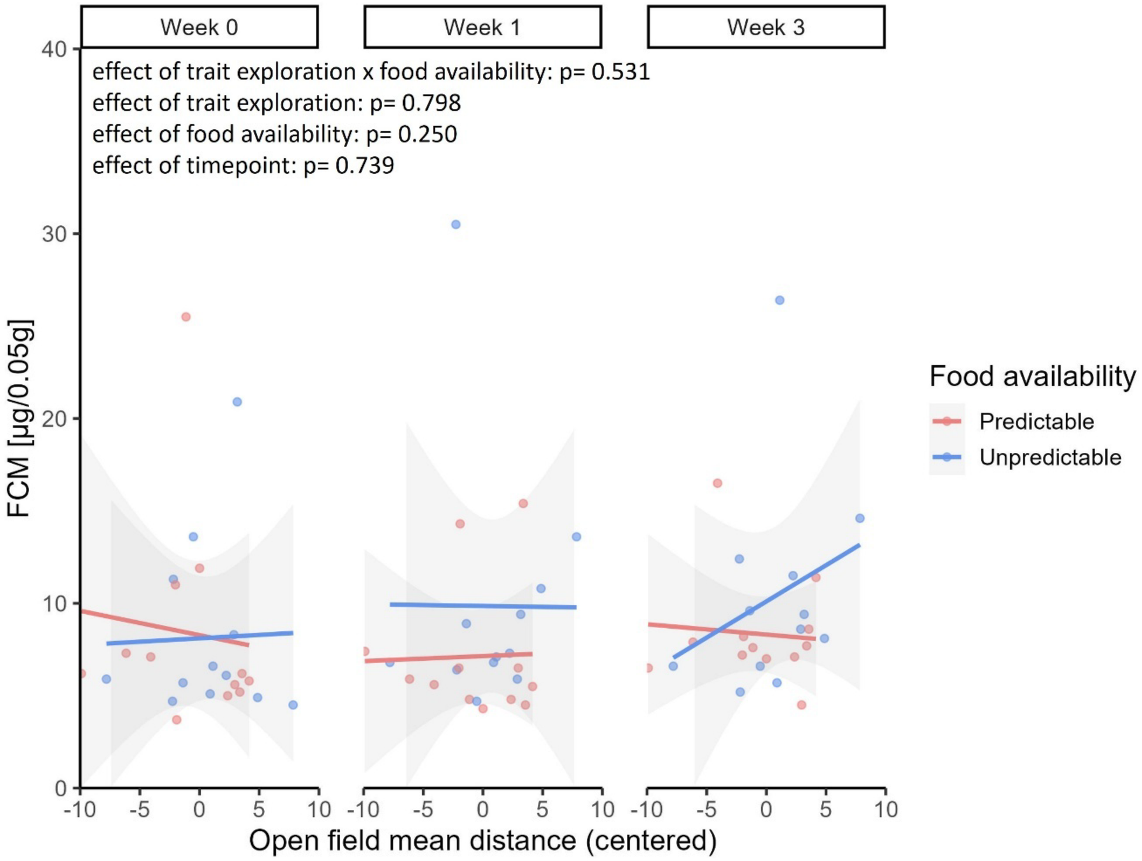

Figure 2: Faecal corticosterone metabolites (FCM). Shown is the relationship between trait exploration measured in the Open field (increasing trait exploration from left to right on x-axis) and FCM concentration (y-axis) separated by exposure weeks (facets) and food availability (colours). Points represent individual animals, lines show model-estimated slopes, and shaded areas represent 95% confidence intervals.

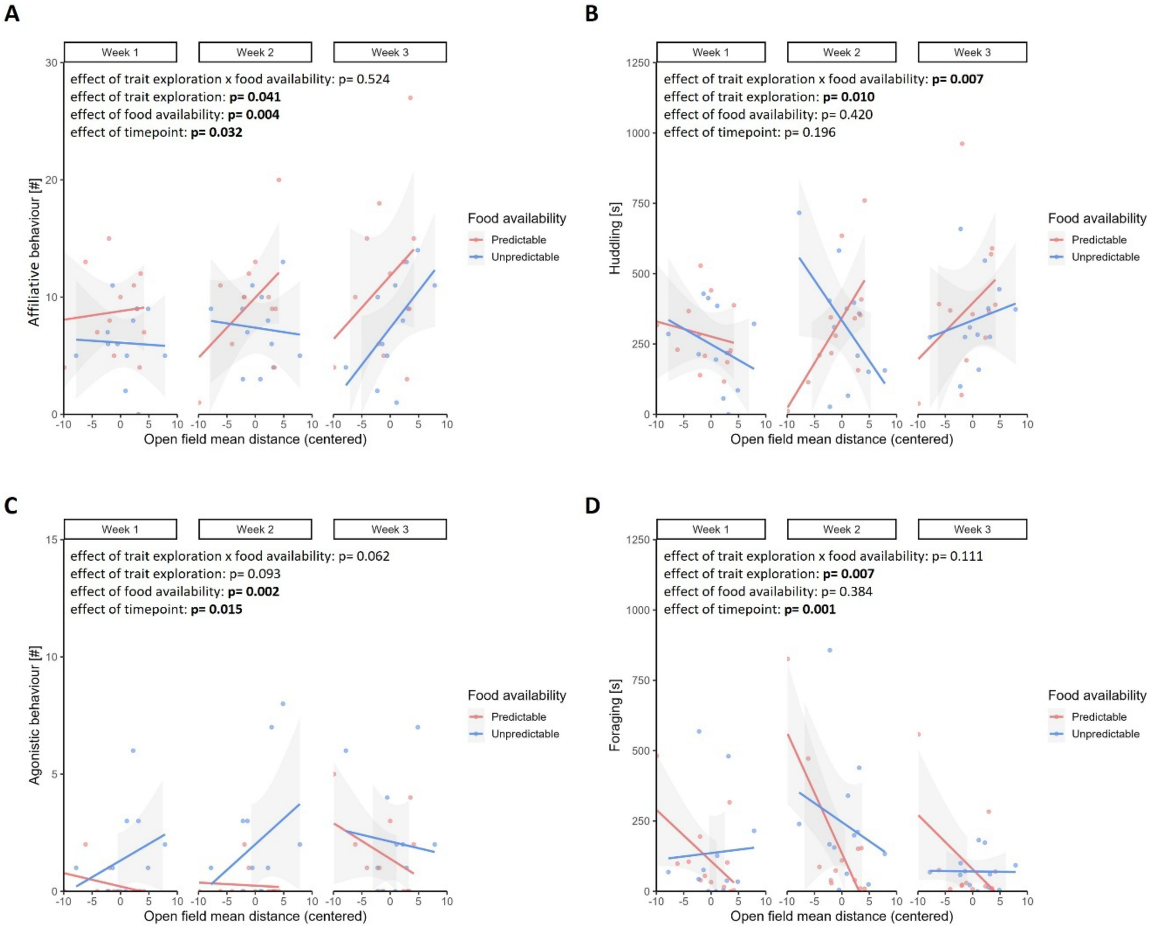

Figure 3: Home cage behaviour. Shown is the relationship between trait exploration measured in the Open field (increasing trait exploration from left to right on x-axis) and (A) the frequency of affiliative behaviour (y-axis) separated by exposure weeks (facets) and food availability (colours), (B) the duration of huddling (y-axis) separated by exposure weeks (facets) and food availability (colours), (C) the frequency of agonistic behaviour (y-axis) separated by exposure weeks (facets) and food availability (colours), (D) the duration of foraging (y-axis) separated by exposure weeks (facets) and food availability (colours). Points represent individual animals, lines show model-estimated slopes, and shaded areas represent 95% confidence intervals.

Furthermore, the analysis concerning the tests for anxiety-like behaviour revealed a significant effect of trait exploration x food availability regarding the sum of entries made to the arms of the Elevated plus maze (EPM) ($\chi2 = 9.455$, df = 1, $p = 0.002$) and a trend for such an interaction effect concerning the entries made to the arena of the Free exploration test (FET) ($\chi2 = 3.189$, df = 1, $p = 0.074$) (Fig. 4). In fact, with increasing trait exploration, individuals made significantly more entries to the arms of the EPM under unpredictable food availability conditions (slope estimate = 0.058 ± 0.014, CI: [0.031, 0.086]). In contrast, in an environment with a predictable food availability, they made less entries (slope estimate = -0.001 ± 0.013, CI: [-0.026, 0.025]). This resulted in a significant difference between the two environmental conditions (slope comparison estimate = -0.059 ± 0.019, z = -3.075, p = 0.002). Regarding the FET arena entries, higher trait exploration was associated with more arena entries in both environmental conditions. However, the relationship was stronger and significant only for the predictable food availability condition (predictable food availability: slope estimate = 0.074 ± 0.024, CI: [0.028, 0.120]; unpredictable food availability: slope estimate = 0.018 ± 0.021, CI: [-0.024, 0.059]), resulting in a trend for a difference between environmental conditions (slope comparison estimate = 0.056 ± 0.032, z = 1.786, p = 0.074). The analysis of the remaining parameters from the EPM and FET did not reveal a significant effect of trait exploration x food availability (for details see supplementary material).

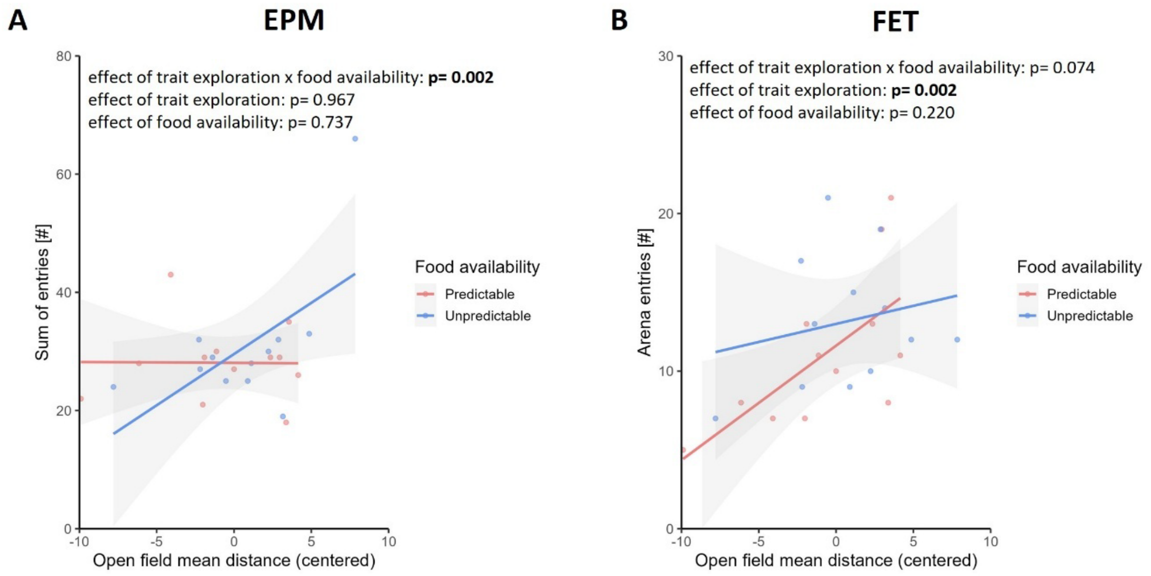

Figure 4: Elevated plus maze (EPM) and Free exploration test (FET). Shown is the relationship between trait exploration measured in the Open field (increasing trait exploration from left to right on x-axis) and (A) the sum of arm entries in the EPM (y-axis) separated by food availability (colours), (B) the number of arena entries in the FET (y-axis) separated by food availability (colours). Points represent individual animals, lines show model-estimated slopes, and shaded areas represent 95% confidence intervals.

Personality main effects

While the analysis of FCMs did not detect a significant effect for trait exploration alone ($\chi2$ = 0.066, df = 1, p = 0.798) (Fig. 2), HCB was found to be affected by the animals' personality. Specifically, an effect of trait exploration was noted for *Affiliative behaviour* ($\chi2$ = 4.191, df = 1, p = 0.041) and *Foraging* ($\chi2$ = 7.378, df = 1, p = 0.007) (Fig. 3). Moreover, there was a trend for an effect of trait exploration on *General activity* ($\chi2$ = 2.832, df = 1, p = 0.092). Here, highly explorative individuals showed significantly more affiliative behaviour (estimate = 0.044 ± 0.021, z = 2.047, p = 0.041), spent less time foraging (estimate = -0.950 ± 0.350, t = -2.716, p = 0.013) and tended to have a higher activity in general (estimate = 0.366 ± 0.217, t = 1.683, p = 0.108), indicating wide-ranging behavioural differences in individuals with varying personality. By contrast, trait exploration did not affect any of the behavioural parameters from the EPM and FET significantly (for details see supplementary material).

Environment main effects

Similar to the FCM findings above, no significant effect of food availability was detected concerning this parameter (χ2 = 1.323, df = 1, p = 0.250), indicating an overall robustness of this endocrinological measure to personality-dependent and environmental influences (Fig. 2). Regarding HCB, the analysis revealed a significant effect of food availability on *Affiliative behaviour* (χ2 = 8.359, df = 1, p = 0.004), with individuals displaying more affiliative behaviours under a predictable food availability (estimate = 0.367 ± 0.127, z = 2.891, p = 0.004) (Fig. 3). Concerning the tests for anxiety-like behaviour, no significant effects of food availability were found. Nevertheless, there was a trend for an effect of food availability on the latency to enter the arena in the FET (χ2 = 2.982, df = 1, p = 0.084). However, post hoc analysis did not detect a significant difference between the predictable and unpredictable condition (estimate = 27.200 ± 15.800, t = 1.720, p = 0.103). For an overview of statistical information, please see supplementary material.

Timepoint main effects

Also for timepoint, the analysis of FCMs did not detect a significant effect (χ2 = 0.606, df = 2, p = 0.739) (Fig. 2). Again, effects on HCB were found, with timepoint significantly affecting *Affiliative behaviour* (χ2 = 6.906, df = 2, p = 0.032), *Agonistic behaviour* (χ2 = 8.450, df = 2, p = 0.015) and *Foraging* (χ2 = 14.689, df = 2, p = 0.001) (Fig. 3). According to the post hoc comparisons, affiliative interactions were less common in exposure week 1 than in exposure week 3 (estimate = -0.261 ± 0.099, z = -2.621, p = 0.024), while agonistic interactions were more common in exposure week 1 than in exposure week 3 (estimate = -0.765 ± 0.271, z = -2.828, p = 0.013). Moreover, foraging behaviour showed a peak in exposure week 2 (week 1 versus week 2: estimate = -3.090 ± 1.270, t = -2.433, p = 0.049; week 2 versus week 3: estimate = 4.810 ± 1.270, t = 3.781, p = 0.001) (p > 0.05 for the remaining comparisons, for details see supplementary material).

Experiment 2: matched versus mismatched social partner

Characterisation phase

In line with the results from experiment 1, the repeatability analysis for characterising the animals regarding their exploratory locomotion in the OF showed temporally consistent inter-individual differences (R = 0.446, CI: [0.171, 0.660], p < 0.001), indicating exploratory locomotion to be a consistent personality trait.

Exposure phase

Personality-by-environment interaction effects

Regarding the analysis of FCMs, no significant effect of trait exploration x social partner was found (χ2 = 0.007, df = 1, p = 0.933) (Fig. 5). Likewise, the analysis of HCB did not show a significant interaction effect between trait exploration and social partner for any of the behavioural parameters recorded (for details see supplementary material).

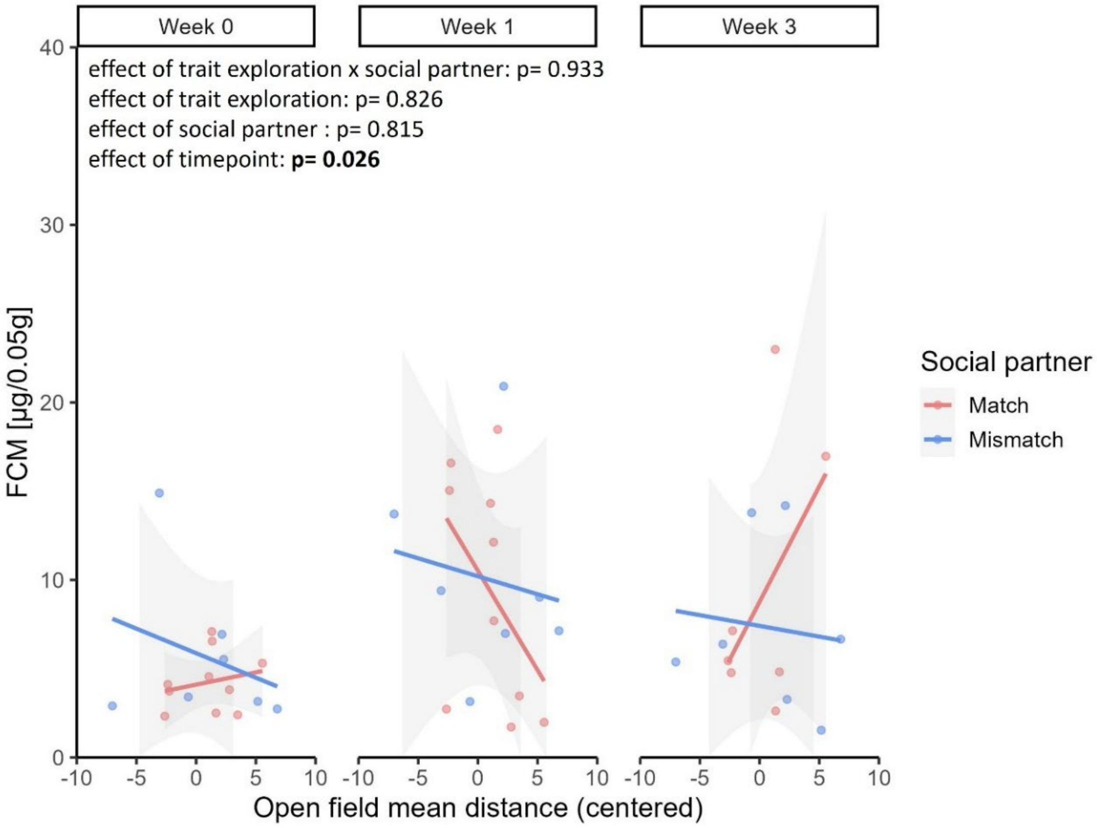

Figure 5: Faecal corticosterone metabolites (FCM). Shown is the relationship between trait exploration measured in the Open field (increasing trait exploration from left to right on x-axis) and FCM concentration (y-axis) separated by exposure weeks (facets) and social partner (colours). Points represent individual animals, lines show model-estimated slopes, and shaded areas represent 95% confidence intervals.

However, the tests for anxiety-like behaviour revealed a significant effect of trait exploration x social partner on the total distance travelled in the EPM (χ2 = 4.632, df = 1, p = 0.031) and the entries made into the arena of the FET (χ2 = 10.230, df = 1, p = 0.001) (Fig. 6). Post hoc analysis detected a significant positive relationship between trait exploration and the total distance travelled in the EPM for individuals housed with a mismatched social partner (slope estimate = 0.460 ± 0.175, CI: [0.077, 0.842]) and a negative relationship on a descriptive level for matched pairs (slope estimate = -0.334 ± 0.398, CI: [-1.206, 0.537]). However, the slopes from the two environmental conditions did not differ significantly (slope comparison estimate = -0.794 ± 0.455, t = -1.746, p = 0.109). Furthermore, animals with a higher trait exploration showed significantly more entries to the FET arena when housed with a mismatched social partner (slope estimate = 0.065 ± 0.017, CI: [0.032, 0.099]). This relationship differed significantly from the one in the environment with a matched social partner, where animals with a higher trait exploration entered the FET arena less often on a descriptive level (slope estimate = -0.070 ± 0.037, CI: [-0.142, 0.003]; slope comparison estimate = -0.135 ± 0.042, z = -3.198, p = 0.001), indicating differences in anxiety-like behaviour depending on the combination of personality in one cage. Furthermore, there was a trend for an effect of trait exploration x social partner regarding the distance travelled on the open arms of the EPM ($\chi2$ = 3.153, df = 1, p = 0.076) and the sum of entries made to the arms of the EPM ($\chi2$ = 3.643, df = 1, p = 0.056), both parameters reflecting locomotor activity. However, no significant results were detected in the post hoc analysis concerning EPM open arm distance (matched social partner: slope estimate = -0.050 ± 0.056, CI: [-0.173, 0.073]; mismatched social partner: slope estimate = 0.041 ± 0.025, CI: [-0.013, 0.095]; slope comparison estimate = -0.0.991 ± 0.064, t = -1.430, p = 0.182). Nevertheless, for the sum of EPM arm entries, a significant positive relationship with trait exploration was found in mismatched pairs (slope estimate = 0.033 ± 0.012, CI: [0.009, 0.058]). This positive association showed a statistical trend to differ from the relationship found in matched pairs, where more explorative individuals showed fewer EPM arm entries on a descriptive level (slope estimate = -0.021 ± 0.025, CI: [-0.070, 0.029]; slope comparison estimate = -0.054 ± 0.028, z = -1.909, p = 0.056).

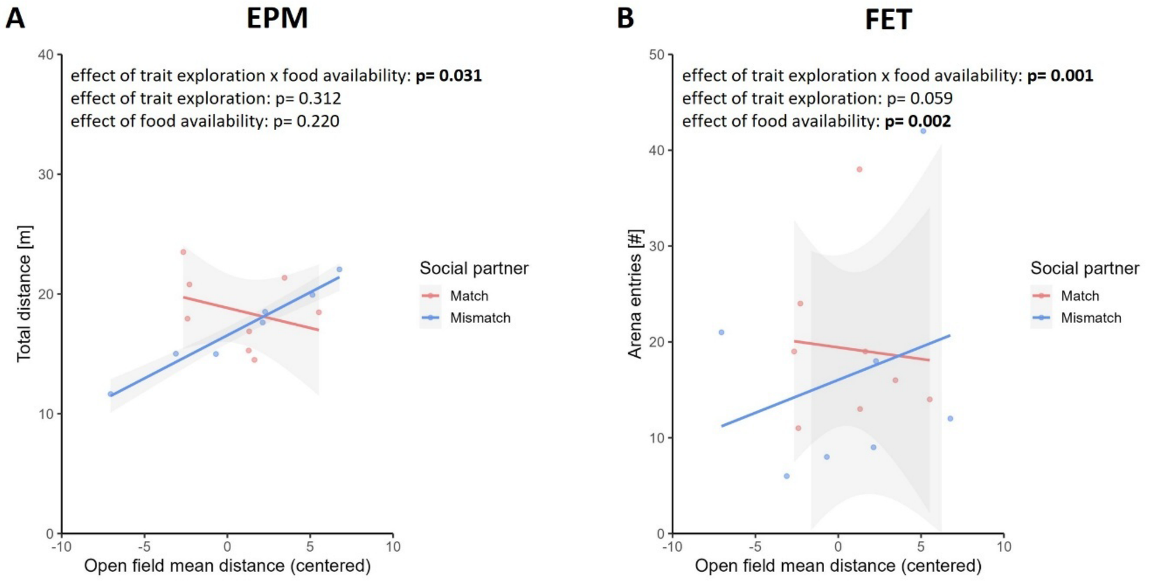

Figure 6: Elevated plus maze (EPM) and Free exploration test (FET). (A) Shown is the relationship between trait exploration measured in the Open field (increasing trait exploration from left to right on x-axis) and (A) the total distance travelled in the EPM (y-axis) separated by social partner (colours), (B) the number of arena entries in the FET (y-axis) separated by social partner (colours). Points represent individual animals, lines show model-estimated slopes, and shaded areas represent 95% confidence intervals.

Personality main effects

Also for trait exploration alone, no significant effect on FCMs was detected (χ2 = 0.048, df = 1, p = 0.826) (Fig. 5). Likewise, no significant effect of trait exploration was found for the HCB and regarding the EPM and the FET (for details see supplementary material).

Environment main effects

Regarding an impact of the social partner, the analysis of FCMs did not reveal a significant effect (χ2 = 0.055, df = 1, p = 0.815), again reflecting a high robustness of this endocrinological parameter to personality-dependent and environmental influences (Fig. 5). Also for HCB, no significant effect of social partner alone was found. Yet, there was a trend for an effect of social partner on *Affiliative behaviour* (χ2 = 3.450, df = 1, p = 0.063), with matched pairs tending to show more affiliative behaviour than mismatched pairs (estimate = 0.393 ± 0.211, z = 1.858, p = 0.063) (Fig. 7).

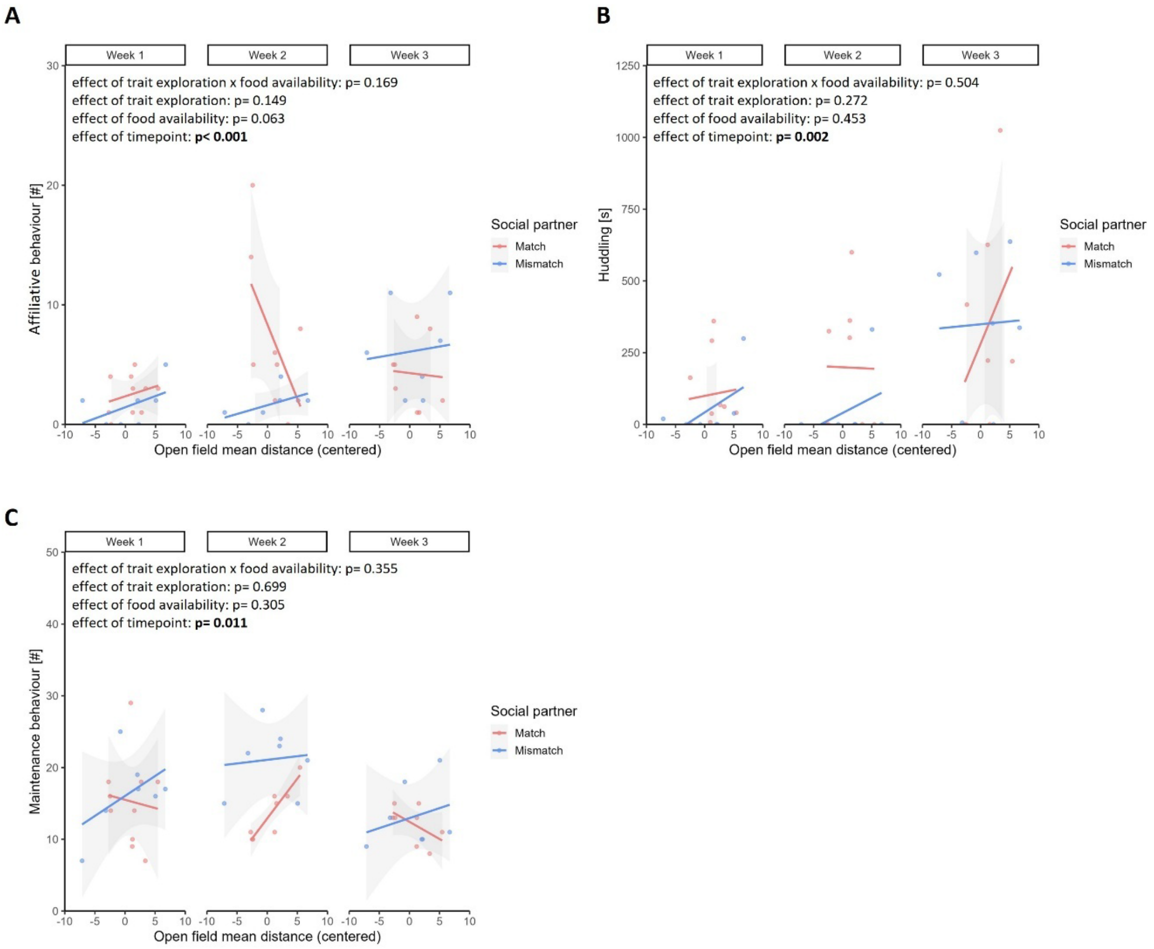

Figure 7: Home cage behaviour. Shown is the relationship between trait exploration measured in the Open field (increasing trait exploration from left to right on x-axis) and (A) the frequency of affiliative behaviour (y-axis) separated by exposure weeks (facets) and social partner (colours), (B) the duration of huddling (y-axis) separated by exposure weeks (facets) and social partner (colours), (C) the frequency of maintenance behaviour (y-axis) separated by exposure weeks (facets) and social partner(colours). Points represent

individual animals, lines show model-estimated slopes, and shaded areas represent 95% confidence intervals.

In the tests for anxiety-like behaviour, the social partner was found to affect the distance travelled in the arena of the FET (χ2 = 9.288, df = 1, p = 0.002). Here, animals housed with a matched social partner travelled greater distances than animals housed with a mismatched social partner (estimate = 15.200 ± 5.590, t = 2.727, p = 0.019). In addition, there was a trend for an effect of social partner on the latency to enter the arena of the FET (χ2 = 3.379, df = 1, p = 0.066) and time spent there (χ2 = 3.543, df = 1, p = 0.060), both parameters that reflect anxiety-like behaviour. However, a significant difference was detected for neither of the two parameters in the post hoc analysis (FET arena latency: estimate = -31.900 ± 19.400, t = -1.645, p = 0.127; FET arena time: estimate = 94.800 ± 56.300, t = 1.685, p = 0.119). For an overview of statistical information, please see supplementary material.

Timepoint main effects

The FCM analysis revealed a significant effect of timepoint (χ2 = 7.337, df = 2, p = 0.026), with post hoc analysis showing that adrenocortical activity was significantly lower before regrouping the animals according to their environmental condition compared to the first week after the regrouping (estimate = -0.755 ± 0.283, t = -2.669, p = 0.031) (Fig. 5). This indicates an impact of the change in environmental condition on HPA axis activity (p > 0.05 for the remaining comparisons, for details see supplementary material). Moreover, in the analysis of HCB, timepoint had a significant effect on *Affiliative behaviour* (χ2 = 21.969, df = 2, p < 0.001), *Huddling* (χ2 = 12.029, df = 2, p = 0.002) and *Maintenance behaviour* (χ2 = 8.934, df = 2, p = 0.011) (Fig. 7). Regardless of social partner, animals showed a higher frequency of affiliative behaviours in exposure week 2 and 3 compared to exposure week 1 (week 1 versus week 2: estimate = -0.808 ± 0.197, z = -4.090, p < 0.001; week 1 versus week 3: estimate = -0.871 ± 0.195, z = -4.454, p < 0.001) and longer durations of huddling in exposure week 3 compared to exposure weeks 1 and 2 (week 1 versus week 3: estimate = -9.250 ± 2.980, t = -3.101, p = 0.011; week 2 versus week 3: estimate = -8.892 ± 3-050, t = -2.915, p = 0.018). Moreover, maintenance behaviour of the animals decreased from exposure week 2 to exposure week 3 (estimate = 0.279 ± 0.094, z = 2.973, p = 0.008) (p > 0.05 for the remaining comparisons, for details see supplementary material).

Discussion

The aim of the present study was to investigate personality-dependent adjustments to different environmental conditions. Therefore, animals were characterised regarding their trait exploration and exposed to an environment with a predictable versus an unpredictable food availability in experiment 1 as well as to an environment with a social partner of matching versus mismatching personality, i.e. trait exploration, in experiment 2. In the characterisation phase, consistent inter-individual differences in trait exploration were found for both experiments. While personality, environment and the interaction of both did not affect FCMs in neither of the experiments, several behavioural adjustments were detected. In fact, experiment 1 revealed an effect of personality x food availability concerning the affiliative, agonistic and maintenance behaviour in the home cage as well as regarding anxiety-like behaviour and locomotor activity in the EPM and FET. Moreover, an effect of personality alone was noted for foraging, activity and affiliative behaviour in the home cage, the latter being also affected by food availability alone. Additionally, experiment 2 detected an effect of personality x social partner in the tests for anxiety-like behaviour and an effect of the social environment on affiliative behaviour in the home cage as well as on locomotor activity in the FET.

Exploratory locomotion was a consistent personality trait in both experiments

In line with the literature, the characterisation performed in both experiments showed temporally consistent inter-individual differences in the rats’ exploratory locomotion measured within the OF, indicating this behaviour to reflect a consistent personality trait (Quante et al., 2025). Thus, the findings add to the body of empirical evidence regarding temporally consistent behaviour in the OF (e.g. Améndola et al., 2022; Herde & Eccard, 2013; Mazza et al., 2018; Réale et al., 2007; Santicchia et al., 2022; Wirowska et al., 2024; Yuen et al., 2017). Besides consistent individual differences in anxiety-related behaviours (e.g. time spent close to the walls of the OF arena versus the centre) that are often used to assess boldness, this finding particularly underscores the existence of differences in spatial exploration among rats. As mentioned in the introduction, such consistent personality traits might have been pressured by natural selection, as they allow appropriate responses on an average level when unlimited behavioural plasticity is too costly (Bergmüller & Taborsky, 2010; Wolf & Weissing, 2010, 2012). Especially in social-living species, behavioural consistency is likely to be advantageous as it increases the predictability of the interaction partner (Cabrera et al., 2021). Although exploration is not a social behaviour per se, consistent individual differences still might have been favoured due to exploration being linked to social behaviour (Aplin et al., 2013; Hakataya et al., 2023; further discussed below).

Personality-dependent adjustment to the environment was found for behavioural measures but not regarding HPA axis activity

In experiment 1, individuals with a higher trait exploration were characterised by more huddling in the predictable food availability condition. Moreover, higher trait exploration was associated with less agonistic and less maintenance behaviour in this condition. The decrease in maintenance behaviour could be explained by an indirect effect of the increased huddling, as socially more integrated animals presumably have a higher chance of being allo-groomed. At the same time, the increase in huddling together with the decrease in agonistic interactions are likely to reduce energetic costs, both by lowering investment in fighting and by supporting more efficient thermoregulation (e.g. Vavrušková et al., 2022). Since energetic savings constitute a fitness advantage for the individual animal, this finding might point towards a better behavioural adjustment of highly explorative animals to predictable conditions. Although increased huddling has also been reported in response to stress (Muroy et al., 2016), other findings that would have indicated elevated stress levels, such as reduced general activity (Blanchard & Blanchard, 1969) or increased HPA axis activity (Amaral et al., 2010), were not detected in the present study, arguing against this interpretation. In an unpredictable environment, in contrast, such behavioural adjustments might not have been possible, due to a constant change in resource availability.

In line with the home cage behaviour results, the tests for anxiety-like behaviour revealed higher trait exploration to be associated with more FET arena entries in the predictable food availability condition. As more FET arena entries are widely interpreted as an indicator of reduced anxiety-like behaviour, this might point towards improved welfare in these animals (e.g. Hurst & West, 2010). Taken together, these findings support the assumption that more explorative individuals perform better in predictable environmental conditions (Benus et al., 1991; Verbeek et al., 1994). From a population level perspective, such inter-individual variation might be beneficial, as it increases resilience to fluctuating environmental conditions (Réale et al., 2007; Sih et al., 2012; Wolf & Weissing, 2012).

Although, the literature often describes less explorative animals to adjust better to unstable environmental conditions (Benus et al., 1991; Verbeek et al., 1994), the present study did not report clear evidence that low trait exploration animals performed better in the unpredictable condition. This might be due to the unpredictable condition constituting a more drastic change in housing condition. In fact, all animals were used to *ad libitum*, i.e. very predictable, feeding before the start of the exposure phase. The stress caused by this environmental change might have impeded the detection of personality-dependent differences, as it was shown that moderate stress decreases inter-individual variation in behavioural and physiological measures (Macrì et al., 2007). In fact, the only finding reported in the unpredictable food availability condition was an association between higher trait exploration and more EPM arm entries, reflecting increased locomotor activity. This increase could be caused by a stronger motivation for foraging under unpredictable food availability conditions, which is in line with previous findings, reporting a mildly restricted feeding routine to decrease anxiety-like behaviour and to increase exploratory locomotion (Quante et al., 2023).

In experiment 2, personality x environment interactions were only detected in the behavioural tests. More specifically, higher trait exploration was associated with more EPM arm entries and a greater distance travelled there as well as more FET arena entries in mismatched pairs. These behavioural differences indicate reduced anxiety-like behaviour and hint towards a better adjustment of highly explorative individuals to a mismatched social partner, when following a traditional interpretation (e.g. Hurst & West, 2010). However, this interpretation is not further supported by the results from the home cage behaviour, where no interaction effects were observed. Moreover, the interpretation contrasts the finding that matching pairs engaged more in affiliative behaviours independent of personality in the home cage (further discussed below).

A reason for this rather weak evidence of personality-dependent adjustments to the social environment might be the presence of only one social partner in the present study. Indeed, researchers assume that effects of the social environment critically depend on the number of group mates (Brehm & Mortelliti, 2024; Krause & Ruxton; Graeme D., 2002) and previous studies have already reported on personality x social environment effects in larger groups (e.g. Magnhagen & Staffan, 2005). Thus, future studies are advised to include larger group sizes to investigate potential personality x social environment effects.

Personality affected behavioural measures in the home cage but not HPA axis activity

In both experiments, trait exploration did not affect HPA axis activity determined by FCM measurements (Palme, 2019). In the literature, divergent findings regarding a link between personality and HPA axis activity are reported. While traditional coping style models describe personality-dependent differences in hormone profiles, with more bold and active individuals typically showing lower basal corticosterone levels and HPA axis reactivity (Carere et al., 2003; Cockrem, 2007; Koolhaas et al., 1999; Mazza, Dammhahn, et al., 2019), further studies report no such link (Sroka et al., 2024) or a context-specific pattern (Mazza, Jacob, et al., 2019). Due to the inconsistent study results, researchers proposed an updated coping style model supporting the idea that physiological and behavioural measures might be more decorrelated in an individual's reaction to environmental challenges than previously assumed (e.g. Koolhaas et al., 2010; Mazza, Dammhahn, et al., 2019; Westrick et al., 2019). Hence, animals with a similar behavioural response, such as the same level of exploration, may vary in their HPA axis activity (e.g. Sroka et al., 2024; Van Reenen et al., 2005; Westrick et al., 2019).

Another explanation for the inconsistent findings may lie in the different tests and parameters used to characterise the animals, as they are likely to measure different aspects of boldness, exploration and activity (Krebs et al., 2019; Sroka et al., 2024). Consequently, two parameters assumed to measure boldness, might not necessarily correlate and differ in their associations with other behavioural and physiological measurements. This is supported by the present study, where EPM and FET measures were unaffected by personality in both experiments, a pattern also reported by other studies comparing multiple tests for anxiety-like and exploratory behaviour (Carter et al., 2012; O'Leary et al., 2013; Yuen et al., 2017).

In experiment 1, personality-dependent differences were found with respect to home cage behaviour. Specifically, individuals with a higher trait exploration were characterised by more affiliative behaviour and general activity but less foraging behaviour. In general, the findings add to the already existing reports of personality-dependent behavioural differences in the literature (Koolhaas et al., 1999; Sroka et al., 2024; Verbeek et al., 1996). While increased general activity is likely to be a direct expression of higher trait exploration, less foraging behaviour could be an indirect consequence of more time spent displaying other behaviours, such as object manipulation and affiliative behaviours. Indeed, a similar finding is reported in a study on bank voles, where individuals were characterised as shy or bold based on several measures, including exploration (Mazza, Jacob, et al., 2019). In this study, bolder individuals (also characterised by more exploratory behaviour) spent less time foraging. The authors suggest that this finding is mainly caused by a higher foraging efficiency in these individuals (Mazza, Jacob, et al., 2019). Regarding the link between trait exploration and affiliative behaviour, a study conducted in birds found personality-dependent differences in social strategies, with fast-exploring birds establishing more but weaker and short-lived social bonds compared to slow-exploring birds that had less but stronger and persistent social associations (Aplin et al., 2013). In this study, it is suggested that these differences reflect the slow-exploring individuals' preference for a safer environment. Smaller social groups may provide more safety by reducing pathogen exposure and improving group-level predator defence, for example through alarm calling. In line with this, a link between exploration and social relationships has recently been reported in rats, with more explorative animals engaging more in the formation of social bonds to conspecifics (Hakataya et al., 2023). Similar to the suggestion above, the authors of the study assume that this is due to more explorative animals being more likely to seek novel and unfamiliar conspecifics. In summary, the observed personality-dependent differences could indicate a higher flexibility in the establishment of social relationships in more explorative individuals, which is likely to be advantageous under changing social environmental conditions.

The fact that no such differences were observed in experiment 2 of the present study, might be explained by the differences in housing condition and food availability, as here, individuals were pair-housed and fed *ad libitum*. While group size is known to particularly affect social interactions (Monfils et al., 2024), both factors, i.e. group size and feeding routine, are known to alter activity levels (e.g. Feige-Diller et al., 2020; Pinelli et al., 2017; Quante et al., 2023). Thus, these factors might have concealed personality-dependent effects on the affiliative behaviour and general activity of the animals in experiment 2.

Environment affected the affiliative behaviour in the home cage

In both experiments, environmental condition was found to affect the rats' affiliative behaviour in the home cage. Although agonistic behaviour decreased and affiliative behaviour increased across the exposure phase of experiment 1, affiliative behaviours were generally more frequent in the predictable food availability condition. This may result from consistent feeding times facilitating more social interactions, as animals quickly habituate to predictable feeding schedules (e.g. Quante et al., 2023). In contrast, the unpredictable food availability might have reduced affiliative behaviours, as rats perceive it as aversive and prefer a predictable over an unpredictable food delivery (Prokasy, 1956; for a review on effects of predictability see Bassett & Buchanan-Smith, 2007). However, this interpretation is not further supported by the measured FCM levels that usually increase in response to stress (e.g. Amaral et al., 2010) but remained unaffected in the present study.

Likewise, experiment 2 revealed increasing affiliative behaviours across the exposure phase, especially in matched pairs. The results are in line with previous studies in primates, reporting individuals with more similar personality types to form closer social bonds (Massen & Koski, 2014), indicating the principle of homophily to also apply to adult female rats. While other studies have demonstrated this phenomenon in relation to other characteristics, such as sex, age, strain and playfulness in juveniles, our study shows homophily to be also present regarding a more fundamental personality trait with high ecological relevance, i.e. exploration (Hakataya et al., 2023; Lampe et al., 2019; Mauri et al., 2022).

Moreover, the tests for anxiety-like behaviour found individuals from matched pairs to travel a greater distance in the arena of the FET. As in this test the animals can freely choose to enter the arena, the increase in exploratory locomotion also implies a reduction in anxiety-like behaviour. As mentioned before, this finding can be interpreted as an indicator of good welfare (e.g. Hurst & West, 2010), pointing towards a welfare-improving effect of housing individuals with matched personality together. Furthermore, the experiment also pointed towards an effect of social group on the welfare of animals. Specifically, a temporal increase in basal corticosterone levels after regrouping the animals into pairs was detected. Following the traditional interpretation (e.g.

Amaral et al., 2010), the finding indicates that either the change in social group or the reduction in group size might have acted as a stressor for the animals. This is in line with previous studies, demonstrating rats in general and female rats in particular to be very social animals that prefer to live in stable groups comprising several individuals (Hackenberg et al., 2021; Patterson-Kane et al., 2004).

Conclusion

The present study reproduces and emphasises previous findings regarding consistent inter-individual differences in rats' exploratory locomotion, encouraging the use of trait exploration for further investigations regarding the consequences of personality traits. By demonstrating that personality and environment jointly shape behavioural adjustment in rats, while physiological responses remain largely independent, the study moreover supports revised suggestions on coping style models. These models propose a greater independency of behavioural and physiological measures than previously assumed. Furthermore, the detected positive association between exploration and affiliative behaviour indicates personality-dependent patterns of social interaction that may influence group structure and social organisation. Additionally, the principle of homophily is shown to apply regarding trait exploration. Together with the finding that social group and feeding routine affects animal welfare indicators, this emphasises the relevance of considering both personality and environment in further research regarding the refinement of housing conditions for animals held in captivity. In summary, the findings highlight the importance of integrating personality into eco-evolutionary perspectives on adjustment processes as well as into animal welfare endeavours.

Author statement

S.H.R. conceived the study. S.H.R., S.K. and S.M.Q. designed the experiments. S.H.R. and S.K. supervised the project. D.Z. and S.M.Q. carried out the experiments. S.M.Q. conducted the statistical analysis of the data. S.M.Q. wrote the initial draft of the manuscript. All authors critically revised the manuscript and gave final approval for publication.

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Declaration of competing interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

Animal health statement

The mentioned and unexpected health problems that occurred in experiment 2 encompassed four females that were excluded from the study at varying time points. All females showed abnormalities in health condition due to one or more bladder stones causing urinary blockage. The breeder was contacted immediately to inquire about such problems in the strain's stock, which was denied. The authors would like to emphasise that none of the rats was part of a manipulation other than what is stated in the manuscript. Moreover, the health status of all animals was carefully monitored by experimenters, animal caretakers and vets before, during and beyond the experiment, ensuring that obtained data is unaffected by any compromising health conditions.

Ethogram for home cage behaviour

Inactivity	*Inactive (s)*	The rat does not show any locomotion or movement for at least three seconds, except for breathing or tiny ear or whisker movements. The behaviour is often accompanied by lying down. The behaviour ends when the rat shows locomotion for at least three seconds or any of the other defined behaviours.
General activity	*Climb (s)*	The rat grabs the grid of the cage with at least three paws and moves along it. The behaviour ends as soon as none of the paws touch the cage bars anymore.
	Object manipulation (s)	The rat interacts with the cage enrichment or nest material and manipulates it with its snout or limbs. The behaviour ends when there is no more manipulation for at least three seconds.
Affiliative behaviour	*Rough & tumble play (#)*	Two rats interact with each other by hopping and pinning each other on the ground by using the forepaws. The behaviour ends, when the pinned rat is on all four paws again.
	Allo-grooming (#)	The rat touches the fur of another rat with its snout for at least three seconds; licking movements may occur. The behaviour ends as soon as there is a distance of at least one snout length between the snout and the body of the conspecific or if the snout is not touching the conspecific for at least three seconds.
	Being allo-groomed (#)	The rat is groomed by another rat (see definition above).
	Huddling (s)	At least two rats are inactive while having body contact for at least three seconds and at least one side of one rat's body touches the side of

		another rat’s body. The behaviour ends as soon as contact ceases for more than three seconds.
Agonistic behaviour	*Chasing (#)*	A rat runs after another rat, which runs in front of it, with a distance between the rats of less than one body length. The behaviour ends as soon as the distance between the rats is more than one body length or the race is interrupted for at least three seconds.
	Being chased (#)	The rat is chased by another rat (see definition above).
	Biting (#)	The rat touches the body of another rat and pinches the skin with its teeth. Every pinch is counted separately.
	Being bitten (#)	The rat is bitten by another rat (see definition above).
	Fighting (#)	At least two rats kick and wrestles each other in fast movements. The rats may produce squeaking noises.
	Mounting (#)	The rat lays its upper body on the back of another rat. The front paws grab the sides of the body of the recipient rat. The rat may show pelvic thrusts.
	Being mounted (#)	The rat is mounted by another rat (see definition above).
Maintenance behaviour	*Feeding (#)*	The rat touches a pellet with its snout and/or forepaws and jaw movements are seen. The behaviour ends, when no jaw movements are seen for at least three seconds.
	Foraging (s) (Only recorded in experiment 1)	The rat inspects the food bowl or the feeder adapter with its snout and/or limbs for at least three seconds. The behaviour ends, when the rat moves away from the food bowl or feeder adapter by at least one snout length or if *Feeding* starts (see definition above).
	Drinking (#)	The rat touches the water bottle with its snout and licking movements are seen. The behaviour ends, when no licking movements are seen for at least three seconds.
	Grooming (#)	The rat moves front limbs or snout in sweeping motions over its body and/or tail. The behaviour ends, when there are no such movements for at least three seconds.
Abnormal behaviour	*Bar mouthing (#)*	The rat places a cage bar between its jaws and gnaws on the bar for at least three seconds. The behaviour ends as soon as the snout moves away from the bar by at least one snout length or the jaw movements are interrupted for at least three seconds.

Supplementary tables

Supplementary Table 1: Statistical information for experiment 1. Statistical information given: data family used for analysing and transformation applied (sqrt = square root transformation). Main effect of interaction and fixed effects ((G)LMM: X^2-value, df = degrees of freedom, p-value). HCB = Home cage behaviour, FCM = faecal corticosterone metabolites, EPM = Elevated plus maze, FET = Free exploration test.

Experiment 1: predictable vs. unpredictable food availability														
Test	**Parameter**	**Data family (Transformation)**	**Exploratory locomotion x food availability**			**Exploratory locomotion**			**Food availability**			**Timepoint**		
			X^2	df	p	X^2	df	p	X^2	df	p	X^2	df	p
HCB	Inactivity	Gaussian (sqrt)	1.119	1	0.290	0.966	1	0.326	0.154	1	0.694	5.549	2	0.062
	General activity	Gaussian (sqrt)	2.105	1	0.147	2.832	1	0.092	0.344	1	0.558	1.222	2	0.543
	Affiliative behaviour	Poisson	0.406	1	0.524	4.191	1	0.041	8.359	1	0.004	6.906	2	0.032
	Huddling	Gaussian (sqrt)	7.335	1	0.007	6.665	1	0.010	0.651	1	0.420	3.261	2	0.196
	Agonistic behaviour	Poisson	3.471	1	0.062	2.819	1	0.093	9.765	1	0.002	8.450	2	0.015
	Maintenance behaviour	Poisson	3.788	1	0.052	2.510	1	0.113	1.356	1	0.244	3.489	2	0.175
	Foraging	Gaussian (sqrt)	2.536	1	0.111	7.378	1	0.007	0.756	1	0.384	14.689	2	0.001
	Bar mouthing	Poisson	-	-	-	-	-	-	-	-	-	-	-	-
FCM		Gaussian	0.391	1	0.531	0.066	1	0.798	1.323	1	0.250	0.606	2	0.739
EPM	Relative open arm time	Gaussian	0.337	1	0.562	0.458	1	0.499	0.995	1	0.318	-	-	-
	Relative open arm entries	Gaussian	2.658	1	0.103	0.999	1	0.318	0.005	1	0.945	-	-	-
	Open arm distance	Gaussian	1.682	1	0.195	0.083	1	0.773	0.004	1	0.949	-	-	-
	Sum of arm entries	Poisson	9.455	1	0.002	0.002	1	0.967	0.113	1	0.737	-	-	-
	Total distance	Gaussian (sqrt)	0.518	1	0.472	0.151	1	0.697	0.356	1	0.551	-	-	-
FET	Arena latency	Gaussian	1.104	1	0.293	1.621	1	0.203	2.982	1	0.084	-	-	-
	Arena entries	Poisson	3.189	1	0.074	9.853	1	0.002	1.505	1	0.220	-	-	-
	Arena time	Gaussian (sqrt)	0.088	1	0.767	0.174	1	0.677	0.252	1	0.616	-	-	-
	Arena distance	Gaussian	0.061	1	0.805	2.432	1	0.119	0.772	1	0.380	-	-	-

Supplementary Table 2: Statistical information for experiment 2. Statistical information given: data family used for analysing and transformation applied (sqrt = square root transformation). Main effect of interaction and fixed effects ((G)LMM: X^2-value, df = degrees of freedom, p-value). HCB = Home cage behaviour, FCM = faecal corticosterone metabolites, EPM = Elevated plus maze, FET = Free exploration test.

Experiment 2: matched vs. mismatched social partner														
Test	**Parameter**	**Data family (Transformation)**	**Exploratory locomotion x social partner**			**Exploratory locomotion**			**Social partner**			**Timepoint**		
			X^2	df	p	X^2	df	p	X^2	df	p	X^2	df	p
HCB	Inactivity	Gaussian (sqrt)	2.137	1	0.144	0.554	1	0.457	0.397	1	0.529	2.695	2	0.260
	General activity	Gaussian (sqrt)	1.682	1	0.195	0.096	1	0.757	0.814	1	0.367	3.909	2	0.142
	Affiliative behaviour	Poisson	1.896	1	0.169	2.078	1	0.149	3.450	1	0.063	21.969	2	< 0.001
	Huddling	Gaussian (sqrt)	0.447	1	0.504	1.208	1	0.272	0.564	1	0.453	12.029	2	0.002
	Agonistic behaviour	Poisson	0.082	1	0.775	0.067	1	0.796	0.089	1	0.766	1.186	2	0.553
	Maintenance behaviour	Poisson	0.856	1	0.355	0.149	1	0.699	1.051	1	0.305	8.934	2	0.011
	Bar mouthing	Poisson	0.610	1	0.435	0.027	1	0.869	1.363	1	0.243	1.241	2	0.538
FCM		Gaussian (sqrt)	0.007	1	0.933	0.048	1	0.826	0.055	1	0.815	7.337	2	0.026
EPM	Relative open arm time	Gaussian (sqrt)	0.358	1	0.550	0.129	1	0.719	1.890	1	0.169	-	-	-
	Relative open arm entries	Gaussian (sqrt)	0.890	1	0.346	1.716	1	0.190	0.241	1	0.624	-	-	-
	Open arm distance	Gaussian (sqrt)	3.153	1	0.076	1.173	1	0.279	0.125	1	0.724	-	-	-
	Sum of arm entries	Poisson	3.643	1	0.056	0.666	1	0.415	0.561	1	0.454	-	-	-
	Total distance	Gaussian	4.632	1	0.031	1.021	1	0.312	1.502	1	0.220	-	-	-
FET	Arena latency	Gaussian	0.093	1	0.760	0.289	1	0.591	3.379	1	0.066	-	-	-
	Arena entries	Poisson	10.230	1	0.001	3.574	1	0.059	9.186	1	0.002	-	-	-
	Arena time	Gaussian	0.128	1	0.721	0.594	1	0.441	3.543	1	0.060	-	-	-
	Arena distance	Gaussian	1.355	1	0.244	0.502	1	0.479	9.288	1	0.002	-	-	-