



Short- and long-term effects of endogenous cortisol on personality traits and behavioural syndromes

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ARTICLE INFO

Article history:

Received 19 July 2023

Initial acceptance 3 November 2023

Final acceptance 16 January 2024

MS. number: 23-00383R

Keywords:

animal personality
behavioural variation
glucocorticoids
repeatability
sex-specific behavioural syndrome
trait covariance

Animals express consistent individual differences in some behaviours, termed animal personality, but behaviours can also vary considerably within individuals, within minutes or hours, due to environmental stimuli. Consistent among-individual variation is often assumed to be mediated by hormonal mechanisms. Hormones are also involved in flexible and fast responses towards environmental stimuli. Even though basic mechanisms by which hormones regulate behaviours are known, much of the quantitative patterns underlying hormone–behaviour interactions within and among individuals remain unclear. Here, we conducted two experiments to investigate the immediate, short-term effects of experimentally elevated cortisol titres on well-known animal personality traits (experiment 1) and their potential long-term effects (experiment 2) in the medium-sized cavy, *Cavia aperea*. Therefore, we tested how personality traits related to stress coping, novelty seeking and social behaviour react within hours to elevated cortisol. In experiment 2, we tested whether a 3-week elevation of cortisol affects the same personality traits after cessation of the hormone treatment. We investigated effects on the mean levels of behaviours, that is, the personality type, the temporal consistency (i.e. repeatability) and among-individual correlations of traits. In experiment 1, we found cortisol led to more aggressive behaviour and more passive stress coping while other traits were unaffected. In experiment 2, we found no long-term effects. Both measured hormones, cortisol and testosterone, showed correlations with several personality traits; these correlations, however, were unaffected by the cortisol treatment. Animals receiving the cortisol treatment showed higher repeatability for one stress-coping trait and lower repeatability for testosterone concentration. Interestingly, the sexes differed in only few mean trait expressions but showed different correlation structures across traits. Taken together, our data indicate that personality traits in adult individuals are very consistent and only react with short-term fluctuations to internal hormonal signals.

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Individuals ubiquitously express consistent differences in behaviours, called animal personality (Dingemanse & Wolf, 2010; Stamps & Groothuis, 2010a, 2010b; Wolf & Weissing, 2012), with personality traits being related, for example, to foraging behaviour and resource use (Svanbäck & Bolnick, 2007; Toscano et al., 2016) and dispersal (Cote et al., 2010). Such consistent behavioural differences have been shown to have ecological as well as evolutionary consequences at the individual and population level by acting on survival and reproduction of individuals (Dall et al., 2012;

Wolf & Weissing, 2012). Recently, evidence has been accumulating that this behavioural variation may be causally related to individual differences in circulating hormone concentrations (Angelier et al., 2009; Cockrem et al., 2010; Hau et al., 2016; Hau & Goymann, 2015). To improve our understanding of the role of hormones in shaping and maintaining personality differences, we need to elucidate the quantitative patterns of hormone–behaviour relationships.

Hormones are good candidates for regulating complex phenotypic changes due to their pleiotropic potential (Ketterson & Nolan, 1992; Zera et al., 2007). Many hormones can affect phenotypes in a long-term way (organizational effects), often during early development. Exposure to glucocorticoids such as corticosterone during

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early life, for example, leads to increased activity and novel environment exploration (both well-known personality traits in birds) in adult Japanese quail, *Coturnix coturnix japonica* (Zimmer et al., 2013). The sex steroid testosterone is a key hormone involved in regulating sexual behaviour and aggressiveness in territorial and reproductive contexts, increasing, for example, female aggressiveness against potential secondary females during the breeding period in European starlings, *Sturnus vulgaris* (Sandell, 2007). In addition to long-term effects, steroid hormones also affect behaviours in a more short-term way (activational effects). These transient effects may last for only minutes to hours as, for example, the behavioural and physiological response to a stressor after activation of the hypothalamic–pituitary axis.

Recently, several studies have demonstrated covariation between hormones, mainly steroid hormones, and animal personality traits (reviewed by Cockrem, 2007; Hau & Goymann, 2015; but see Holtmann et al., 2017). However, the evidence mostly stems from correlative studies and the strength and direction of such associations vary across species, experimental conditions and the respective trait measured, thereby preventing a broad understanding of the underlying mechanisms of such associations (Hau et al., 2016; Hau & Goymann, 2015). Experimental studies are needed to elucidate whether such hormone–behaviour associations are common across the animal kingdom and potentially constrain evolution or whether they are specific to certain situations or environmental conditions (Hau & Goymann, 2015). The strong focus on changes in the population average (mean level treatment differences), while effects on within- and between-individual variation remain largely ignored, further hampers an understanding of how endocrine differences affect consistent behavioural differences (but see DiRienzo & Montiglio, 2016; Kok et al., 2019; Royauté & Dochtermann, 2017).

The importance of variation around the mean as the basis on which selection can act has been pointed out long ago (Boake, 1989; Hayes & Jenkins, 1997). The amount of between-individual variation is important, both in estimating the consistency of a trait (i.e. repeatability) and in correlations among traits (i.e. behavioural syndromes). Trait repeatability is considered as a cornerstone of personality research because it often sets an upper boundary for trait heritability and thus reflects the evolutionary significance of a trait (Falconer & Mackay, 1996). Reduced or increased variation between individuals in a certain trait has, in addition, the potential to alter its correlation with other traits, thereby potentially affecting how populations respond to varying selection pressures (Killen et al., 2013; Sih et al., 2012).

Recent studies show that the extent of variation between individuals can be shaped by environmental factors that are often strongly associated with the challenges the environment poses. Nutritional stress during early life, for example, increased variation in activity and exploration between individuals in zebra finches, *Taeniopygia guttata* (Careau et al., 2014) and activity and response to predator cues in field crickets, *Acheta domesticus* (Royauté & Dochtermann, 2017). Low-quality diet often results in elevated baseline glucocorticoid titres (Honarmand et al., 2010; Kitaysky et al., 2001) which is likely to mediate changes in behaviour. Indeed, experimental manipulation of cortisol titres in young wild cavies, *Cavia aperea*, has proven to increase between-individual variation in baseline cortisol and associated stress-coping behaviours until adulthood (Guenther et al., 2018). Likewise, experimental elevation of corticosterone during the nestling stage of zebra finches strengthened correlations between morphological and physiological traits later in life (Merrill & Grindstaff, 2018). So far, few other studies have experimentally investigated the effects of elevated hormone titres on trait variation and its consequences,

i.e. trait repeatability and correlations among traits, rather than changes in average behaviour.

To investigate the short- and long-term effects of experimental cortisol elevation on personality traits, we conducted two experiments in adult wild cavies in captivity. In the first experiment, we measured personality traits and behaviour in the home enclosure over a few hours following the administration of exogenous cortisol (CORT, experiment 1). We investigated whether elevated cortisol titres lead to short-term behavioural changes in the personality traits activity, boldness, aggressiveness and stress coping in a restraint situation. All traits that we studied here have already been shown to be individually long-term stable, that is, to represent personality traits, for this species (see Guenther, Finkemeier, et al., 2014 for boldness; Guenther, Brust, et al., 2014 for sociopositive and aggressive behaviour; Guenther & Trillmich, 2023 for hand escape and struggle test).

In the second experiment we were interested in the long-term effects of cortisol administration on personality traits and behavioural syndromes and followed the adult cavies over 2 months (experiment 2). Here, we aimed to answer the following questions. Does a 3-week elevation of cortisol titres in adult individuals after cessation of the treatment affect (1) the expression of the average personality type (group mean) and/or between- or within-individual variation and repeatability and (2) the strength of behavioural correlations? In addition, during the second experiment we investigated whether the sexes differ in their mean level response to cortisol elevation and, finally, in behavioural syndromes.

As cortisol is one main component involved in the short-term stress response and one of its main functions is to enhance performance under (potentially) threatening or challenging situations (Dhabhar, 2018), we predicted an increase in cortisol would lead in the short term to an increase in the average of stress-related behaviours. Such an increase in the expression of stress-related behaviours should become visible when observing behaviour freely and should also affect the expression of stress-coping personality traits in the short term when tested in challenging situations. An increase in behavioural expression should, for example, become visible when an unknown individual is entering the home enclosure (social encounter test), or when testing the response to human handling (struggle test; hand escape test). At the same time other personality traits, such as boldness (novel object test) or activity should be reduced. In contrast, we predicted no long-lasting effects of cortisol elevation on personality traits of adult individuals as their personality traits should be rather inflexible.

For effects on variation between individuals and correlations among traits, we could expect an increase in behavioural variation comparable to findings in young animals of this species (Guenther et al., 2018). The observed increases were due to greater among-individual variation and affected trait repeatability as well as correlations among traits. Such effects were also observed in a few previous studies and were suggested to be caused by environmental stressors (Killen et al., 2013) or by developmental canalization of traits mediated by hormones (Hoffmann & Woods, 2001). Alternatively, we could expect no change in personality traits of adult individuals as these are relatively stable and do not respond with long-term changes to cortisol manipulation. In addition, but irrespective of the cortisol manipulation, we expected several sex-specific effects on behavioural means and correlations between traits, especially regarding hormone titres and social behaviours since males but not females of this species actively defend territories (Asher et al., 2008). Therefore, we additionally measured plasma testosterone, assuming males would have higher plasma levels of testosterone and be more variable in their behaviour (i.e. within-individual variation) over time.

METHODS

Animals and Maintenance

In total, 14 adult unrelated female cavies were used for experiment 1 and 50 (24 males, 26 females) adult animals were used for experiment 2 (see Fig. 1 for an overview of the experimental timeline). All animals were descendants from a breeding population of wild cavies kept at Bielefeld University, bred and raised under identical laboratory conditions. At the start of the study, all animals were approximately a year old and had prior breeding experience. To allow individual recognition, each animal was marked with a pit tag (ID-100, TROVAN, passive transponder system; Euro ID, Weilerswist, Germany; dimensions: diameter: 2.12 mm; length 11.5 mm) inserted subcutaneously into the interscapular region.

One week before the study, animals were introduced to the experimental housing conditions. At this time, and again directly after completion of all experimental procedures, each individual was weighed.

For experimental housing, the animals were introduced into large enclosures that could house up to three individuals and we usually kept three females together. These enclosures could be

divided into multiple compartments via transparent trap doors, which were closed during the daily experimental procedures. Each compartment measured 0.8 m² and contained a water bottle, a brick stone, a feeder, hay and an opaque shelter. Wood chips served as bedding material. For females, the trap doors were only closed during behavioural testing while males were housed singly to prevent aggression among them. The animals were kept under constant a temperature of $20 \pm 3^\circ\text{C}$ and natural light conditions with additional artificial light from 0600 to 1900 hours. Hay, guinea pig pellets (Höveler, Düsseldorf, Germany) and water were available ad libitum. At least three times a week, the food was supplemented with fresh grass, fruits or vegetables except cucumbers.

Cortisol Manipulation

Based on findings from a previous study (Guenther et al., 2018), an oral application method was used for the cortisol (CORT) elevation. In both experiments, females received 5 mg cortisol powder (Ref. Nr. 352450050; Acros Organics, Antwerp, Belgium) on a slice of cucumber, while males, which are on average slightly heavier than females, received 6 mg. This dosage induced an elevation of plasma CORT levels comparable to an acute stressor (Guenther & Trillmich, 2013) while levels returned to baseline

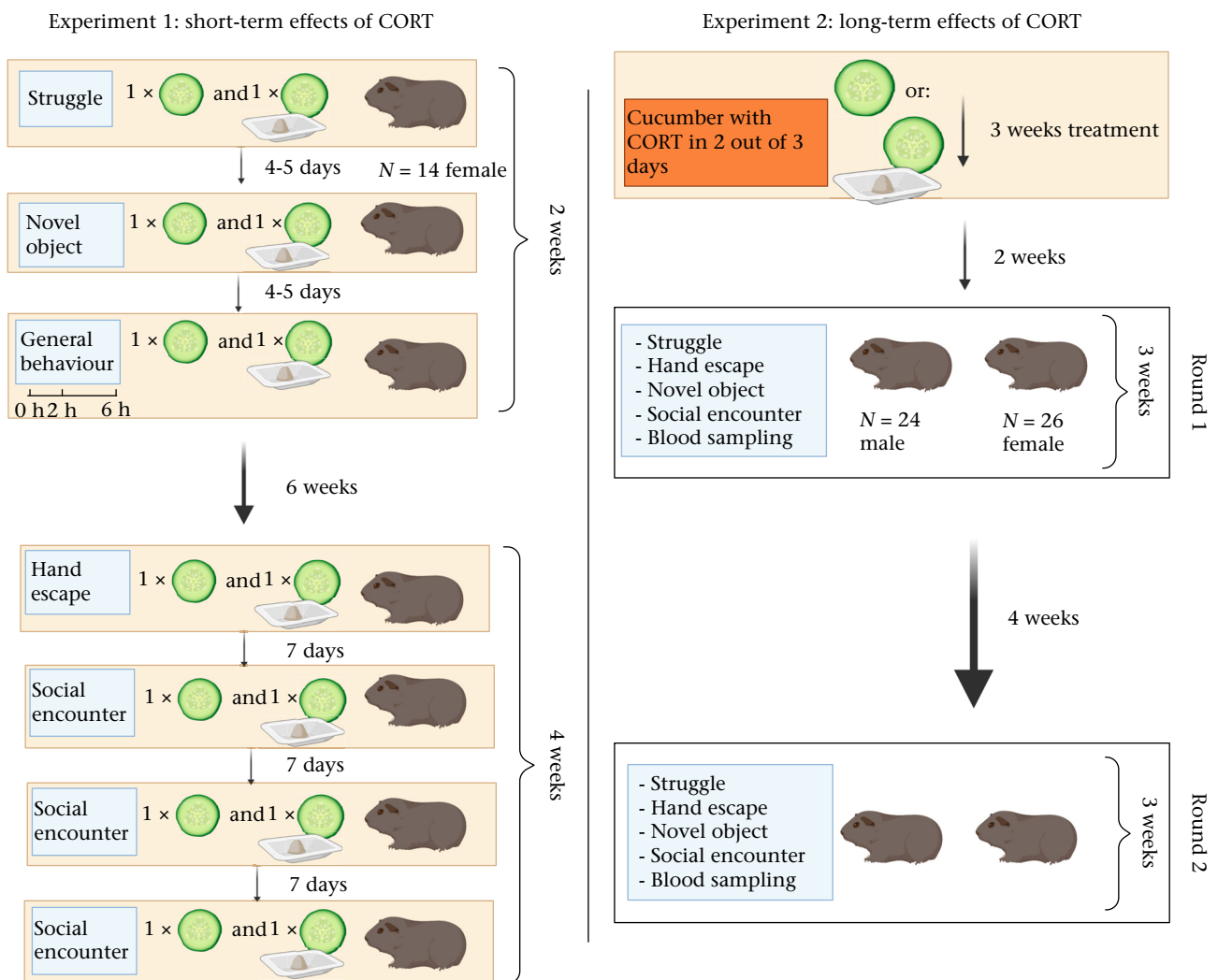


Figure 1. Overview of experimental timelines for experiment 1 (short-term effects of experimentally elevated cortisol (CORT)) and experiment 2 (long-term effects of elevated CORT). Green discs represent slices of cucumber with or without CORT (depicted as powder on a tray). Light blue boxes summarize the traits that were measured. Figure created with BioRender.com.

within 24 h (Guenther et al., 2018). The control treatment received a slice of cucumber without cortisol. On experimental days, individuals were separated by closing the trap doors of the enclosures between 0845 and 0945 in the morning. A slice of cucumber (with or without cortisol) was presented on a brick stone within the enclosure. Every 15 min thereafter, the experimenter checked whether the cucumber had been eaten.

Cortisol administration experiment 1 (short-term effects)

Animals received a single dose of cortisol (or a control cucumber) followed by one of the three behavioural tests (see Fig. 1) so that each animal received the hormone treatment three times and the control treatment three times. After consuming the cucumber, the animal remained separated until completion of the behavioural tests of that day. All animals participated in the behavioural tests under control and treatment conditions with at least 24 h break between the two conditions so that we obtained paired data to increase statistical sensitivity. Cucumbers with and without cortisol were presented alternately so that an animal would not receive a continuous cortisol treatment. If an animal did not consume the cucumber within 105 min, the trial was stopped, and the animal did not participate in behavioural tests that day. To avoid any potential influence of a long-lasting cortisol treatment that might occur when continuing the treatment after the first three hormone manipulations, the animals were given a break of 6 weeks after we had recorded their general behaviour in the home enclosure and their behaviour in the struggle and the novel object tests (see below) before we tested the effect of the hormone treatment in the hand escape and social encounter tests.

Cortisol administration experiment 1 (long-term effects)

Animals received either the cucumber with cortisol or the control on 2 of 3 days for a period of 21 days. This procedure has been shown to result in a robust increase in baseline cortisol levels while avoiding supraphysiological elevation (Guenther et al., 2018). After consuming the cucumber, trap doors were opened, and the animal could then move and interact freely with its group members. All animals sharing an enclosure were assigned to either the control or the treatment condition. In cases ($N = 3$) where animals did not readily consume the cucumber, they remained separated until the evening. In all cases the cucumber was consumed at that time. Behavioural observations started 2 weeks after the end of the 21-day treatment period and were conducted again after a break of 4 weeks.

Behavioural Measurements

All behavioural tests were conducted between 0900 and 1200 hours and between 1400 and 1700 hours as previous studies reported no time-of-day effect during these times (Guenther & Trillmich, 2013). For experiment 2, all behavioural tests (except the social encounter test, see below) were conducted twice, first 2 weeks after the end of the treatment and again 1 month later. The order of tests was conducted in four different sequences in which each test was followed and preceded by each possible other test (Díaz-Uriarte, 2001). The test sequence for each individual was kept constant across successive measurements. In each test round, the animal completed all tests within 2 weeks. To minimize potential carryover effects between tests, animals were left undisturbed for at least 1 day between tests.

General behaviour in the home enclosure (experiment 1)

Females were kept separated after cucumber consumption and their behaviour in the home enclosure was videorecorded for 1 h

immediately after and then 2 h and 6 h after consuming the cucumber. Recordings were done once in the control and once in the treatment condition. The period of activity was scored manually (locomotion and actively performing behaviours as total time within the recorded hour), how often the animal performed behaviours indicating nervousness (i.e. number of jumps, inspecting the trap door, running in circles or digging) and how often it performed maintenance behaviours (number of food intakes, grooming).

Hand escape test (experiments 1 and 2)

The animal was gently taken from its enclosure to be weighed. Thereafter, it was placed on the open hand of the experimenter approximately 5 cm above the ground of its enclosure. The time the animal spent immobile on the hand was measured for 60 s. If the animal had not left the hand within 60 s, it was placed under a shelter in the enclosure and scored the maximum time.

Struggle test (experiments 1 and 2)

After gently picking up the animal from its home enclosure, the experimenter held it on its back in their hand for 30 s. The time the animal spent struggling during this time was measured using a stopwatch.

Novel object test (experiments 1 and 2)

Females were separated from their group by closing the trap door. As males were kept singly, this step was not necessary for them. Then, an unknown object was introduced in the compartment approximately 20 cm away from the shelter. As novel objects we used a green eggcup and a red yoghurt cup. To avoid habituation to a specific object, each animal was presented once with the eggcup and once with the yoghurt cup; the starting object was assigned randomly. The number of times the animal touched the object within 15 min after the first contact was scored as boldness. Boldness measured in this way has been shown to represent a risk-taking behaviour correlated with several other risk-taking behaviours as well as life history variables in this species. Bolder animals are likewise more aggressive (Guenther & Trillmich, 2023), more explorative (Guenther, Finkemeier, et al., 2014) and mature at an earlier age (Guenther, 2018).

Social encounter test (experiments 1 and 2)

For the social encounter test animals were confronted with an unfamiliar conspecific (stimulus animal) of the same sex, which did not participate in any other experiments. In total, six females (experiment 1) and eight (four males, four females in experiment 2) stimulus animals were used so that each animal participated in at most one test per day. An additional shelter was added, so that both animals had the opportunity to hide. The shelters were made of transparent red plastic, so the experimenter could see through it. For the cavies, which cannot perceive red (Jacobs & Deegan, 1994), the shelter appeared dark. The focal animal was separated from its group in a single compartment of its enclosure (for females only). The stimulus animal was introduced to the compartment in which the focal individual was separated, and the behaviour of the focal animal was observed for 15 min. Because the behaviour of the focal animal depends on the behaviour of the stimulus animal, this test was conducted three times under treatment and three times under control conditions (experiment 1) or three times per test round (experiment 2) with different stimulus individuals. The focal animal was confronted with different stimulus animals in a randomized order throughout the period of testing. The number of friendly (naso-nasal and naso-anal sniffing) and aggressive behaviours (attacking, chasing or curved body posture) were recorded using

ethograms based on Rood (1972). In three cases, the tests had to be interrupted due to fighting. In all cases, the focal animal initiated the fight and was scored with the maximum number of aggressive behaviours observed during all tests.

Hormone Analyses (Experiment 2)

In experiment 2, a blood sample was taken from each individual after completion of each round of behavioural testing, that is, around 4 and 8 weeks after the end of the cortisol treatment. Blood samples were taken at 1200 ± 30 min within 3 min of capturing the animal. About 100 μ l of blood were collected from the marginal ear vein of the animal. Plasma was separated after centrifuging for 10 min at 8000 rpm and stored at -20°C until further analyses. All hormone concentrations were analysed in duplicate and averaged for analyses.

Baseline plasma cortisol concentration was measured using a competitive enzyme immunoassay (RE52061 IBL; IBL International GmbH, Hamburg, Germany) using specific antibodies against cortisol. The antibody cross-reacted with the following other steroids: prednisolone 29.8%, 11-desoxycortisol 8.48%, cortisone 4.49%, prednisone 2.12%, corticosterone 1.99%, 6β -hydroxycortisol 1.03%. Samples were evenly distributed across seven assays. The intra-assay % CV was $< 4\%$ and the interassay % CV was $< 8\%$.

Baseline plasma testosterone concentrations were determined using an enzyme immunoassay kit from Demeditec Diagnostics GmbH, Kiel, Germany (DES 6622). The antibody used cross-reacted with relevant steroids as follows: 5α -dihydrotestosterone 23.3%, androstenedione 1.6% and all other tested steroids $< 0.1\%$. The intra-assay CV was $< 7\%$ and the interassay CV was $< 12\%$.

Statistical Analyses

Analyses were conducted using R versions 3.1.2 and 3.5.1 (The R Foundation for Statistical Computing, Vienna, Austria, <http://www.rproject.org>) with the package 'MCMCglmm' for Bayesian mixed models (Hadfield, 2010).

Experiment 1

To investigate the effect of the cortisol treatment on trait mean levels, we constructed univariate Bayesian mixed models (Hadfield, 2010) including treatment (control versus CORT) as fixed and individual ID as random effect. For the analysis of the general behaviour in the home enclosure, time (0 h, 2 h and 6 h) and the interaction between treatment and time were also fitted. For models investigating aggression and friendly social behaviour, stimulus ID was fitted as an additional random effect. Hand escape latency and struggle docility were fitted assuming a Gaussian distribution while a Poisson distribution was assumed for all other variables. We used noninformative inverse-Wishart priors. All models were run for 525 000 iterations, a burn-in of 25 000 and a thinning interval of 500. MCMC-derived P values are used to infer significance of fixed effects. We report the posterior mode along with its 95% credible interval.

Experiment 2

To investigate the effect of the cortisol treatment on trait mean levels, we first constructed a multivariate Bayesian mixed model including all behaviours as well as the two hormones as response variables and treatment, test round, sex and the interaction between sex and treatment as fixed and individual ID as random effect (Hadfield, 2010). An interaction of treatment and test round had only a small, nonsignificant effect size ($\beta = 0.2$, $P_{\text{MCMC}} = 0.31$); thus, we proceeded with the model excluding the interaction term. Hand escape latency, struggle docility, CORT and testosterone were

fitted assuming a Gaussian distribution while a Poisson distribution was assumed for all other variables based on their distribution. We used noninformative inverse-Wishart priors. This and all other models were run for 525 000 iterations, a burn-in of 25 000 and a thinning interval of 500. MCMC-derived P values are used to infer significance of fixed effects. We report the posterior mode along with its 95% credible interval. Model convergence of multivariate models was tested by applying the (Gelman & Rubin, 1992) using three separate chains with overdispersed starting values.

To investigate covariation between traits and trait repeatability, we constructed two multivariate models next, separately for treatment and control animals. These models included all behavioural variables as response variables (applying the same distributions as before), sex as fixed effect and individual ID as random effect. For these models we used slightly informative inverse-Wishart priors and assumed the residual variance to be 10^3 .

To estimate repeatability from the output of these two models separately for control and treatment, we calculated the posterior mode of $R = V(\text{ID})/V(\text{ID}) + V(\text{units})$, with $V(\text{ID})$ being the between-individual variance and $V(\text{units})$ being the within-individual (or residual) variance. A trait is considered repeatable if the credible interval does not include zero.

To compare repeatabilities of control and treatment with each other, we also calculated the MCMC posterior distributions of the differences in repeatability estimates between treatments ($\Delta R = R(\text{control}) - R(\text{cort})$) following Montiglio and Royauté (2014) and Royauté et al. (2015).

Differences in correlations between treatment and control were assessed by calculating the between-individual correlations (r_{bi}) based on the posterior mode of the respective multivariate models (control or treatment). As above, the correlations were compared between treatments ($\Delta r_{\text{bi}} = r_{\text{bi}}(\text{control}) - r_{\text{bi}}(\text{cort})$).

To test for sex-specific repeatability and correlation structure, we calculated multivariate models separately for males and females following the same logic. Likewise, sex-specific repeatabilities were calculated from the variance components of these models and the difference in repeatability was calculated as ($\Delta R = R(\text{males}) - R(\text{females})$). In a similar way, sex-specific correlation patterns were calculated and compared between the sexes: ($\Delta r_{\text{bi}} = r_{\text{bi}}(\text{males}) - r_{\text{bi}}(\text{females})$).

For females, we ran an additional multivariate model including a random effect of enclosure to check for potential block effects. The enclosure variance was estimated to essentially zero and we continued with models not including an enclosure term. Since males were kept singly, enclosure identity and male identity would be 100% confounded and hence we did not run a model to test for the enclosure effect in males.

Ethical Note

Experimental procedures were in accordance with German animal protection laws. Facilities were approved (2014) by the local government authority responsible for health, veterinary and food monitoring (Gesundheits-, Veterinär- und Lebensmittelüberwachungsamt Bielefeld). The experiments were performed under licence 84-02.04.2016.A071 LANUV, NRW, Germany. Animals were allowed to acclimatize to experimental housing conditions for 1 week before starting experimental procedures. Fresh food (carrots, bell pepper, etc.) at least three times a week served as enrichment. Females could be housed in social groups, facilitating natural social behaviour of the species. Adult males are highly aggressive against same-sex conspecifics. To ensure social contact, they were housed with visual, auditory and olfactory contact with females. During social encounter tests, the experimenter was always present in the room to separate animals in case of severe fighting, i.e. animals biting each other. This happened

Table 1

Behavioural responses to elevated cortisol by female caviae shown in the home enclosure immediately and 2 and 6 h after cortisol administration

Variable		Immediate response	2 h	6 h
General activity	C	296.3 (195–395)	121.0 (–184–170)	50 (–184–89)
	T	260.2 (162–350)	96.5 (–118–248)	88.7 (–176–100)
Maintenance behaviours	C	5.0 (–3.6–8.2)	5.1 (1.1–7.3)	2.6 (–3.2–4.4)
	T	5.5 (–3.9–9.3)	5.2 (1.0–7.3)	3.0 (–3.2–4.4)
Nervous behaviours	C	3.4 (2.1–4.6)	2.6 (1.3–3.9)*	2.5 (1.0–3.2)*
	T	3.6 (2.4–4.9)	3.8 (2.4–5.5)	4.2 (2.9–6.0)

General activity was modelled assuming a Gaussian error distribution while maintenance behaviours and nervous behaviours were modelled assuming a Poisson distribution. Reported here are the results from paired, Bayesian t tests as post hoc comparison after the initial mixed-effects model indicated a significant time*treatment interaction (see Table A1). Credible intervals are given in parentheses; asterisks and estimates displayed in bold indicate significant results ($p_{\text{MCMC}} < 0.05$), i.e. credible intervals overlapping in less than 5% of all runs. For full statistical model output see Table A1.

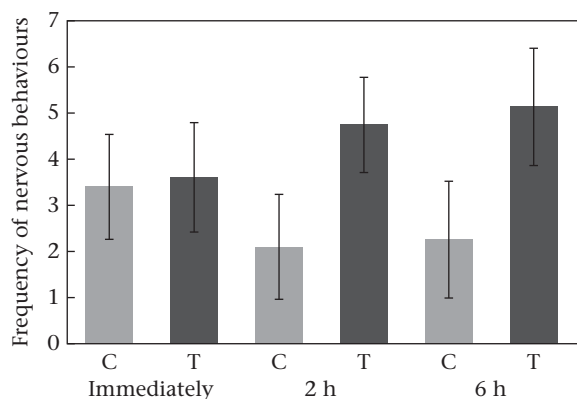


Figure 2. Effects of a single dose of cortisol on the frequency of behaviours indicating nervousness (jumping, rearing, digging) immediately, 2 h and 6 h after cortisol administration. Bars indicate the mean \pm SE of the data. C: control; T: cortisol treatment.

once in experiment 1 (after 10 min) and four times in experiment 2 (after 3–12 min). After we separated the animals, they calmed down quickly and did not need further treatment. The number of animals being tested was estimated based on power analyses prior to the experiment to ensure the use of a minimum number of animals but with high scientific quality at the same time. As effect size for experiment 1, we assumed 0.8, that is, a large effect size based on Cohen following pilot studies (see Guenther et al., 2018) and paired samples. For experiment 2, we used 0.29 as effect size, estimated based on previous experiments (Guenther et al., 2018). Sample sizes were estimated based on the assumption of two groups (control versus treatment) because we did not have any indication to assume sex-specific effects. Power analyses were conducted using the R package 'pwr'. To minimize potential stress through the application of

exogenous cortisol, we specifically developed an oral application technique that does not involve handling and restraining of animals but rather relies on their voluntary participation. Whenever animals had to be handled, for example when transporting them to an experimental test set-up, they were handled only by experienced personnel and with calm and care. Between each test, animals were given at least 24 h break to ensure full recovery from any potentially stressful experience. All animals were maintained for breeding or further experiments after the study.

RESULTS

Experiment 1: Short-term (Activational) Effects of Cortisol

A single dose of cortisol did not affect the overall level of activity or the amount of maintenance behaviours such as resting and feeding during the 6 h period after administration (Table 1, Table A1). However, it increased nervous behaviours such as jumping, digging and rearing from 2 h after treatment onwards (Table 1, Fig. 2). It also reduced the amount of struggle behaviour ($P_{\text{MCMC}} = 0.03$) and increased the latency to escape from the observer's hand ($P_{\text{MCMC}} = 0.04$; see Table A2, Fig. 3a, b). It did not affect boldness but increased the amount of overt aggressive interactions with an unknown conspecific ($P_{\text{MCMC}} = 0.02$; Fig. 3c).

Experiment 2: Long-term Effects of Cortisol

Effects on average personality (mean trait values)

Prolonged treatment with repeated doses of cortisol for 3 weeks did not affect body mass or any of the physiological or behavioural traits recorded (Table 2). Females had overall higher baseline cortisol concentrations but lower testosterone concentrations than males (Table 2). Males showed more aggressive behaviour in the social encounter tests than females (Table 2).

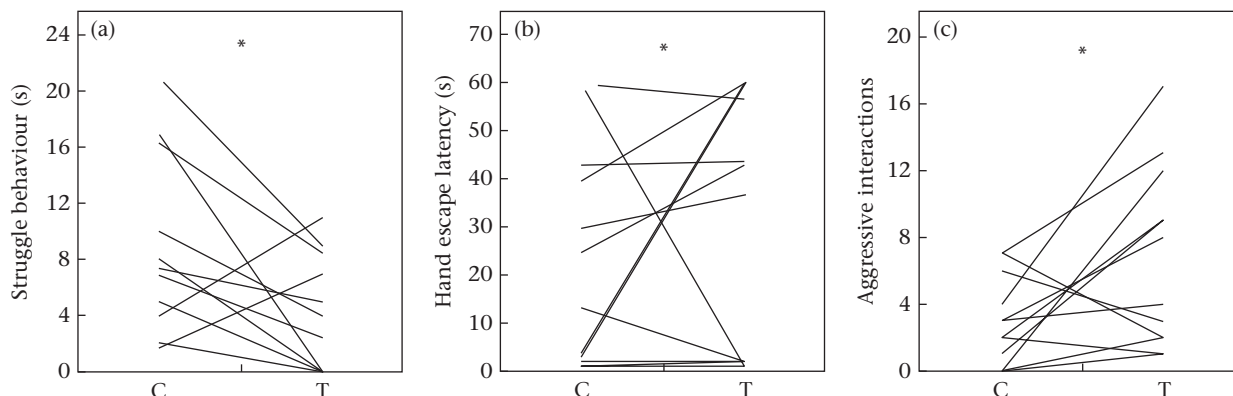


Figure 3. Effects of a single dose of cortisol on (a) struggle behaviour, (b) latency to escape from the observer's hand and (c) number of aggressive interactions shown. C: control; T: cortisol treatment.

Table 2

Experiment 2: Effects of treatment and sex on mean trait expression after long-term cortisol treatment

Trait	Treatment (control as reference)	Sex (females as reference)	Treatment*Sex	Mean values (raw data)
Body mass	−20.57 (−96.19+68.77)	27.83 (−50.47+101.73)	56.20 (−60.77+152.40)	639.7 g
Cortisol	−175.30 (−370.52+5.49)	−328.82 (−484.91−134.92)*	179.57 (−67.67+437.38)	M: 602.6 ng/ml F: 925.9 ng/ml
Testosterone	−227.37 (−653.45+195.07)	302.43 (107.45–731.33)*	68.02 (−592.53+612.17)	M: 813.0 pg/ml F: 475.2 pg/ml
Hand escape latency	1.70 (−10.84+14.98)	2.35 (−9.87+15.23)	0.13 (−18.95+19.21)	12.3 s
Struggle behaviour	4.20 (−1.13+9.66)	3.24 (−2.87+7.93)	−2.34 (−9.41+6.17)	2.4 s
Boldness	−0.52 (−1.31+0.23)	−0.58 (−1.32+0.11)	0.31 (−0.80+1.34)	9 touches in 1 h
Friendly behaviour	1.00 (−0.46+2.43)	1.17 (−0.25+2.50)	−0.69 (−2.60+1.11)	1.19 interactions in 1 h
Aggression	0.86 (−1.50+1.16)	8.87 (6.44–14.19)*	−0.16 (−0.24+0.69)	0.77 interactions in 1 h

Estimates are derived from one Bayesian multivariate mixed model. Posterior means and credible intervals are shown. Estimates marked by an asterisk and displayed in bold are regarded as significant (i.e. credible intervals do not include zero).

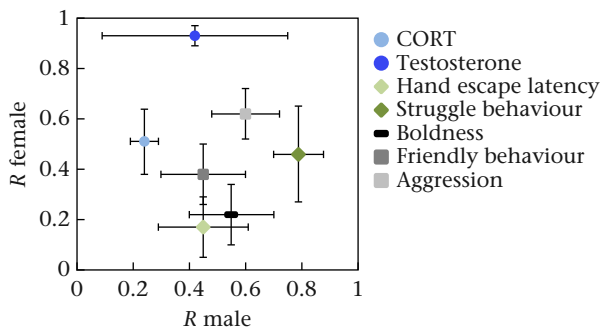


Figure 4. Sex-specific repeatability estimates (R) averaged across control and treatment. Point estimates are given with their corresponding 95% credible intervals. Hormone traits are displayed in blue, stress-coping behavioural traits are displayed in green and other behavioural traits are displayed in black/grey.

Treatment-dependent changes in repeatability and syndrome structure

The repeatability of testosterone concentration calculated across both sexes was reduced in the treatment group (control: $R = 0.94$, credible interval = 0.90–0.97; treatment: $R = 0.22$, credible interval = 0–0.49; $P_{\text{MCMC}} = 0.02$; see also Fig. 4, the unusually high R value is strongly driven by females) while the repeatability

of struggle behaviour was higher in the treatment group (control: $R = 0.41$, credible interval = 0.26–0.56; treatment: $R = 0.79$, credible interval = 0.68–0.92; $P_{\text{MCMC}} = 0.03$). For testosterone, the reduced repeatability arose from an increase in within-individual variation, while we observed an increase in between-individual variation for struggle docility (Table A3). The treatment did not affect repeatability in any other trait. Cortisol treatment did not affect any correlations between traits in a statistically significant way (Table 3).

Sex-specific effects on repeatability and syndrome structure

Males showed lower repeatability estimates compared to females for both hormones while they had higher repeatability estimates for all nonsocial behavioural traits, that is, struggle docility, hand escape latency and boldness (Fig. 4). No difference in repeatability estimates for social behaviours were found.

Behavioural syndromes were in general very similar between males and females with the exception that males showed a stronger positive correlation between boldness and friendly behaviour (female: $R = -0.07$, credible interval = −0.44–0.43; males: $R = 0.75$, credible interval = 0.55–0.92; Fig. 5, Table A4) and a stronger negative correlation between friendly behaviour and latency to escape from the observer's hand (female: $R = -0.03$,

Table 3Experiment 2: correlation estimates (r_{bi}) for caviae treated with cortisol for 3 weeks (T) and control animals (C)

Traits	$r_{\text{bi}}(\text{C})$	CI_{C}	$r_{\text{bi}}(\text{T})$	CI_{T}	$P(\Delta r_{\text{bi}})$
CORT–testosterone	0.18	−0.1:0.46	−0.12	−0.42:0.18	0.33
CORT – hand escape latency	−0.38*	−0.74:−0.02	−0.62*	−0.88:−0.22	0.18
CORT – struggle behaviour	−0.32*	−0.65:0.00	−0.7*	−0.92:−0.30	0.36
CORT – boldness	0.23	−0.18:0.64	0.04	−0.38:0.38	0.48
CORT – friendly behaviour	−0.43*	−0.75:−0.11	0.21	−0.22:0.64	0.22
CORT – aggression	0.39*	0.11:0.67	0.08	−0.33:0.49	0.46
Testosterone – hand escape latency	−0.23	−0.56:0.1	0.17	−0.46:0.8	0.58
Testosterone – struggle behaviour	0.51*	0.23:0.79	−0.27	−0.82:0.28	0.11
Testosterone–boldness	0.28	−0.07:0.63	0.15	−0.33:0.63	0.54
Testosterone – friendly behaviour	0.2	−0.12:0.52	0.07	−0.76:0.9	0.51
Testosterone–aggression	−0.07	−0.33:0.19	−0.14	−0.53:0.26	0.36
Hand escape latency – struggle behaviour	−0.31	−0.69:0.07	−0.74*	−0.96:−0.52	0.42
Hand escape latency–boldness	−0.61*	−0.95:−0.27	−0.1	−0.30:0.42	0.4
Hand escape latency – friendly behaviour	−0.28	−0.67:0.11	0.01	−0.39:0.41	0.55
Hand escape latency–aggression	−0.2	−0.5:0.1	0.03	−0.38:0.44	0.45
Struggle behaviour–boldness	0.28	−0.12:0.68	−0.1	−0.52:0.24	0.35
Struggle behaviour – friendly behaviour	0.53*	0.22:0.84	−0.08	−0.47:0.31	0.28
Struggle behaviour–aggression	−0.23	−0.51:0.05	0.2	−0.1:0.5	0.39
Boldness – friendly behaviour	0.36	−0.02:0.74	−0.18	−0.52:0.16	0.45
Boldness–aggression	0.15	−0.16:0.46	−0.12	−0.39:0.15	0.29
Friendly behaviour–aggression	−0.2	−0.49:0.09	−0.31	−0.62:0	0.41

CORT: cortisol; T: testosterone. Point estimates and accompanying credible intervals (CI) are shown separately for the control versus treatment groups. The P values ($P(\Delta r_{\text{bi}})$) indicate whether control and treatment groups differ from each other based on overlap of credible intervals. Correlations whose CIs do not overlap zero are displayed in bold and are marked by an asterisk.

credible interval = -0.41 – -0.35 ; males: $R = -0.54$, credible interval = -0.86 – -0.22 ; Fig. 5). In addition, females showed a stronger relationship between CORT and escape behaviour than males.

DISCUSSION

In this study, we used caviae to test whether (1) an oral application of cortisol, which results in a peak in plasma cortisol about 1 h later, elicits short-lasting behavioural reactions, (2) an elevation of cortisol over 3 weeks would affect aspects of animal personality such as mean phenotypic expression, temporal consistency of traits and among-individual correlations with other traits, that is, behavioural syndromes and (3) males and females differ in their response to the cortisol treatment or generally in personality and/or behavioural syndrome structure. We found the expected short-term reactions of behaviours related to the stress response, that is, struggle behaviour and hand escape latency, while the prolonged CORT treatment did not affect any aspects of personality over the long term. The sexes differed in several aspects such as mean levels, repeatabilities and correlation between traits.

Short- Versus Long-term Effects of CORT

Experimental manipulation of cortisol titres induced short-term (i.e. activational) effects on behaviours related to nervousness and anxiety as well as on behaviours that are often considered to be stress-coping personality traits (i.e. struggle behaviour and escape latency) of adult wild caviae. Under the influence of CORT, individuals shifted from a more proactive stress-coping strategy characterized by the fight-or-flight response (Koolhaas et al., 1999), to a more passive coping strategy in test situations, in which the stressor resembled being caught by a predator (struggle test; latency in hand escape test). Reactive stress coping in these two situations is indicated by a longer duration of freezing behaviour which, in natural situations, minimizes the stimulation for the predator to attack and increases the chances of evading it (Curio, 1976; Gallup, 1979). In contrast, in a socially challenging situation, we saw an increase in overt aggressive behaviour indicative of proactive coping. In the social encounter test, the animal was confronted with an unknown conspecific in its own home range; however, as the intruder was not superior in strength or size, an active confrontation strategy might confer an advantage in such a situation (in contrast to a potential predator encounter). Other behaviours, not directly related to coping with challenge, such as

curiosity to investigate a novel object (boldness) or home cage activity in the absence of potential threats, were not affected by the cortisol elevation.

In contrast to the short-term changes in behaviours, there were no effects on behavioural traits remaining 2 weeks after the end of a 3-week period of chronically elevated cortisol. In addition, body mass, baseline cortisol and testosterone titres remained unchanged, indicating that this 3-week exposure did not have any long-term effects on behaviour or physiology of adult animals. However, it is well described that a chronic elevation of glucocorticoids will induce high anxiety-like states and even depression-like syndromes in rodents and humans (Murray et al., 2008; Sterner & Kalynchuk, 2010). Such effects are nonadaptive and often result from severe stressors and/or a hyperactivation of the HPA-axis (Sachar & Baron, 1979). These effects can last for long periods but are usually interpreted as neuropsychiatric disorders and/or chronic stress outside the ecologically relevant situation (Tata & Anderson, 2010). Such circumstances may explain findings from humans in which stressful events in adulthood can have enduring effects on personality (Beltran et al., 2009; Jovanovic & Ressler, 2010). It has been demonstrated that such effects are time and dosage dependent (Sterner & Kalynchuk, 2010). Since the goal of such studies is often to induce depression-like states in animal models, exogenous CORT is usually applied in supraphysiological dosages (e.g. Bonier et al., 2007) while the dosage used in our experiments was within the natural range (Guenther et al., 2018). By providing the CORT treatment in a pulsatile manner and at a dosage reflecting the CORT elevation to a stressful situation (Guenther & Trillmich, 2013), we avoided triggering a feedback mechanism of the HPA-axis leading to a strong decrease in baseline CORT titres (Quispe et al., 2015). Within ecologically relevant situations, glucocorticoids coordinate energy allocation to different functions and are responsible for the maintenance of homeostasis (Romero, 2004). In such situations, acute, stress-induced peak levels of glucocorticoids are downregulated back to baseline levels within hours after the end of the stressor (Sapolsky et al., 2000). When the organism is able to reach homeostasis again, theory does not predict any long-term changes in the phenotypic expression (Romero et al., 2009).

Differences in between-individual correlations between traits should primarily arise as a consequence of genetic correlations changing over evolutionary timescales (Dochtermann & Nelson, 2014; Van Oers et al., 2011) or by irreversible developmental plasticity in early life (Duckworth, 2010; Groothuis & Trillmich,

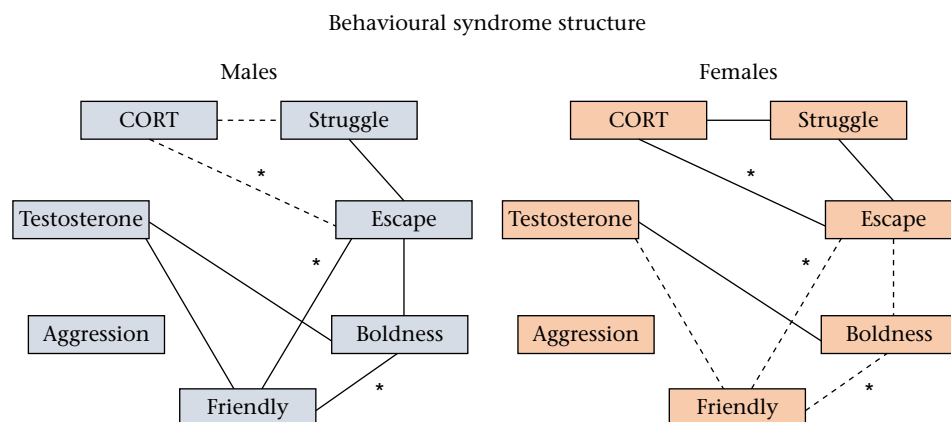


Figure 5. Behavioural syndrome structure for males and females. Solid lines indicate between-individual correlations with credible intervals (CI) not overlapping zero (i.e. significant) and dashed lines indicate correlations with CIs overlapping zero (i.e. nonsignificant). Nonsignificant correlations are displayed if the respective correlation for the opposite sex was significant. Lines marked by an asterisk indicate a difference in correlation estimates for males and females as estimated by r_{bi} . For a complete overview of all sex-specific correlations see Table A4.

2011; Stamps & Groothuis, 2010a, 2010b). During ontogeny, the phenotype is thought to adjust optimally to the environment in which the adult individual needs to survive and reproduce successfully (predictive adaptive response hypothesis, Bateson et al., 2014; Belsky et al., 1991; Gluckman et al., 2005; Nettle et al., 2013). Developmental plasticity is particularly strong during early ontogeny and generally decreases with age (Stamps & Krishnan, 2017). Environmental perturbations experienced in adulthood, on the other hand, usually have reversible, short-term influences, for example through transient changes in multiple traits via hormonal control (Ketterson & Nolan, 1999). Therefore, our findings are in line with our initial hypothesis, that is, expecting short-term fluctuations but no long-term changes to personality traits in response to CORT manipulation in adult animals. Conducting similar experimental manipulations during adolescence led to long-term persistent changes in personality traits associated with stress coping (Guenther et al., 2018), suggesting that this younger life stage indeed shows increased sensitivity to hormonal manipulations compared to the adult stage.

Sex-specific Effects of CORT and Sex-specific Behavioural Syndromes

On average, males had higher testosterone titres and initiated more aggressive behaviours than females when confronted with an unknown conspecific. Females, on the other hand, had a lower baseline CORT concentration than males. The CORT treatment affected males and females similarly for all observed traits, but we found sex-specific effects for repeatability estimates and for correlations among traits. While males showed a higher repeatability for all nonsocial personality traits, we observed no sex difference for social traits and females actually showed higher repeatability for both hormones. For males, boldness in a nonsocial context (novel-object test) and friendly behaviour shown in a social context were significantly positively associated while this was not the case for females. In addition, males that escaped quickly from the experimenter's hand showed more friendly behaviours in a social context while this association was absent in females.

We cannot exclude that any of the observed sex effects were caused by the differences in the housing conditions between males and females. However, theory also predicts that personality differences are caused by life history trade-offs (Biro & Stamps, 2008; Réale et al., 2010; Stamps, 2007). Life history trade-offs and roles often differ between males and females and, hence, sex-specific differences in mean trait expression, temporal consistency and correlation among traits are generally predicted (Hämäläinen et al., 2018; Immonen et al., 2018; Schürch & Heg, 2010). A recent meta-analysis showed that sex-specific differences in phenotypic means and variances were most evident in species with a polygynous mating system such as caviés (Tarka et al., 2018). As a consequence of different outcomes of allocation strategies, repeatability estimates are also predicted to differ between males and females, at least for behaviours closely related to reproduction and in species that exhibit biparental care (Schuett et al., 2010). Indeed, in a meta-analysis, males had generally higher repeatability estimates than females for parental behaviours such as food provisioning, while other behaviours such as activity did not differ between the sexes (Schuett et al., 2010). In line with theoretical predictions (Hämäläinen et al., 2018; Immonen et al., 2018), we here found higher male repeatability for boldness and both stress-coping traits, all of which were previously shown to be tightly connected to reproductive traits in this species (Guenther, 2018). Surprisingly, we found higher repeatability estimates for both hormones in females compared to males, although a recent meta-analysis concluded that repeatabilities of glucocorticoids are in general similar between the sexes (Schoenemann & Bonier, 2018).

However, in their analysis, Schoenemann and Bonier (2018) did not account for differences in mating or parental care system. We suggest that differences in glucocorticoid repeatability may be mediated by the mating and/or parental care system as observed for behavioural traits but apparently in an opposite direction.

So far, only a few studies have investigated whether sex-specific differences in mean trait levels and repeatability translate into sex-specific behavioural syndromes. Fresneau et al. (2014) found a sex-specific syndrome between handling aggression and nestling defence in blue tits, *Cyanistes caeruleus*, while Michelangeli et al. (2016) reported similar behavioural syndromes for males and females despite differences in mean trait expression, suggesting a high evolutionary stability of the syndrome structure. Sex-specific differences in syndrome structure such as those observed here could imply that behaviours are regulated by different physiological pathways or even that the same behaviour is underpinned by completely independent sets of genes in males and females (Immonen et al., 2018; Royauté et al., 2021). An uncoupling of trait expressions between the sexes might suggest that males and females can follow independent evolutionary trajectories rather than being constrained by their shared genomic architecture.

In summary, we have shown that personality traits are very stable against perturbations in adult caviés despite strong short-term effects of exogenous cortisol elevations. The long-term cortisol treatment did not result in physiological or behavioural changes after cessation of treatment, likely due to the manipulation leading to an elevation within the natural range. Furthermore, we found sex-specific differences in temporal consistency as well as in trait correlations in adult individuals, suggesting natural and sexual selection in the past have shaped morphological, physiological and behavioural dimorphism in this species.

Author Contributions

A.G. and A.G.G. conceived the study design. A.G. conducted data collection for experiment 2 and E.G. for experiment 1. A.G. and V.G. conducted all hormone analyses. A.G. conducted statistical analyses and wrote the first manuscript draft. V.G. and A.G.G. commented on the manuscript.

Data Availability

The data accompanying this article are available from Dryad at <https://doi.org/10.5061/dryad.6hdr7sr7c>.

Declaration of 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.

Acknowledgments

We thank Pia Taron for help with the behavioural observations and the animal caretakers, especially Kristina Ruhe, for taking good care of the animals throughout the study. A.G. was funded by a personal Leopoldina Postdoc Scholarship (LPDS 2015-04).

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Appendix

Table A1

Acute response to elevated cortisol of behaviours of female cavies shown in the home enclosure immediately (time 1), 1 h (time 2) and 6h (time 3) after cortisol administration relative to that of the control treatment

Trait	General activity	Comfort behaviour	Nervous behaviour
Intercept (control, time 1)	303.35 (208.05–400.29)	1.20 (0.36–1.85)	3.40 (2.24–4.52)
Treatment	–38.49 (–179.86–88.69)	0.02 (–0.65–0.64)	0.23 (–0.96–1.45)
Time 2 (2 h)	–182.43 (–330.30 – –59.90)*	–0.17 (–0.83–0.44)	–1.30 (–2.46–0.04)*
Time 3 (6 h)	–251.68 (–383.51–116.10)*	–0.86 (–1.59–0.13)*	–2.48 (–3.62–1.17)*
Treatment*time 2 (2 h)	14.10 (–177.21–199.78)	–0.03 (–1.04–0.88)	1.14 (0.84–2.5)*
Treatment*time 3 (6 h)	74.46 (–96.86–285.23)	0.09 (–0.88–1.09)	1.53 (0.39–2.15)*

General activity was modelled assuming a Gaussian error distribution while comfort behaviour and nervous behaviour were modelled assuming a Poisson distribution. Credible intervals are given in parentheses; asterisks indicate significant results ($P_{\text{MCMC}} < 0.05$), i.e. credible intervals not overlapping zero.

Table A2

Acute response to elevated cortisol of behaviours of female cavies shown in the hand escape test (hand escape latency), the struggle test (struggle behaviour), the novel object test (boldness) and the social confrontation test (friendly behaviour, aggression) after cortisol administration relative to that of the control treatment

	Hand escape latency	Struggle behaviour	Boldness	Friendly behaviour	Aggression
Intercept	20.40 (7.3–33.8)	8.64 (5.1–11.7)	1.83 (1.1–2.5)	0.44 (–1.1–0.1)	0.20 (–0.9–0.4)
Treatment	14.57 (3.56–34.4)*	–4.84 (–9.1–0.3)*	0.05 (–0.9–1.1)	–0.50 (–1.4–0.4)	1.34 (0.5–2.3)*

Hand escape latency and struggle behaviour were modelled assuming a Gaussian error distribution while all other behaviours were modelled assuming a Poisson distribution. Credible intervals are given in parentheses; asterisks indicate significant results ($P_{\text{MCMC}} < 0.05$), i.e. credible intervals not overlapping zero.

Table A3

Repeatability (R) estimated for cavies treated with exogenous cortisol for 3 weeks (T) and control animals (C)

Trait	Group	Repeatability			Among-individual variance			Within-individual variance		
		R	CI	$P(\Delta R)^*$	V_{among}	CI	$P(\Delta R)^*$	V_{within}	CI	$P(\Delta R)^*$
Cortisol	C	0.76	0.65–0.87		123.6	27.6–534.1		35.1	7.6–20.28	
	T	0.5	0.35–0.72	0.38	157.4	29.4–209.6	0.14	62.6	15.3–92.2	0.31
Testosterone	C	0.94	0.9–0.97		612.7	127.4–1024.6		331.0	70.0–855.6	
	T	0.22	0–0.49	0.02	211.1	114.1–418.6	0.48	698.3	266.0–887.4	0.02
Hand escape latency	C	0.4	0.21–0.58		13.2	4.1–20.4		17.8	3.3–97.9	
	T	0.32	0.17–0.47	0.63	14.5	5.0–25.2	0.65	20.5	5.5–33.4	0.66
Struggle behaviour	C	0.41	0.26–0.56		2.0	0.53–5.3		2.8	0.47–7.4	
	T	0.79	0.68–0.92	0.03	7.3	1.7–13.8	0.06	1.7	0.32–2.1	0.88
Boldness	C	0.29	0.15–0.44		18.7	6.5–37.3		50.5	8.1–312.7	
	T	0.32	0.09–0.56	0.75	9.3	3.2–19.1	0.21	12.7	3.5–20.1	0.33
Friendly behaviour	C	0.66	0.4–0.75		1.2	0.33–3.19		1.7	0.89–2.1	
	T	0.58	0.46–0.71	0.80	3.2	0.98–8.6	0.61	6.5	1.1–14.1	0.20
Aggression	C	0.4	0.26–0.54		5.5	1.4–25.8		2.8	0.47–17.6	
	T	0.34	0.21–0.49	0.66	4.7	1.2–22.1	0.94	3.4	0.58–21.1	0.65

Point estimates and accompanying credible intervals (CI) are shown separately for the control and treatment groups. The P values ($P(\Delta R)^*$) indicate whether control and treatment groups differ from each other based on overlap of credible intervals. Bold estimates indicate significant differences between treatment and control; estimates in italics indicate trends ($0.09 < P > 0.05$).

Table A4

Sex-specific correlation estimates for males (M) and females (F)

Traits	r_{bi} (M)	CI _(M)	r_{bi} (F)	CI _(F)	$P_{(\Delta r_{bi})}$
CORT–testosterone	–0.38	–0.75: +0.19	0.14	–0.43: +0.44	
CORT – hand escape latency	0.19	–0.39: +0.29	–0.58	–0.91: –0.31	*
CORT – struggle behaviour	–0.02	–0.28: +0.37	0.42	+0.22: +0.68	
CORT–boldness	–0.60	–0.95: –0.33	–0.07	–0.46: +0.21	
CORT – friendly behaviour	–0.25	–0.42: +0.77	0.21	–0.55: +0.60	
CORT – aggression	0.09	–0.17: +0.63	0.15	–0.32: +0.54	
Testosterone – hand escape latency	–0.28	–0.49: +0.31	–0.30	–0.71: +0.19	
Testosterone – struggle behaviour	–0.22	–0.70: +0.41	0.34	–0.28: +0.59	
Testosterone–boldness	0.64	+0.12: +0.73	0.60	+0.23: +0.95	
Testosterone – friendly behaviour	0.62	+0.20: +0.71	–0.03	–0.51: +0.23	
Testosterone–aggression	–0.14	–0.60: +0.32	–0.04	–0.54: +0.18	
Hand escape latency – struggle behav	–0.60	–0.95: –0.21	–0.38	–0.64: –0.07	
Hand escape latency–boldness	–0.50	–0.78: –0.26	–0.06	–0.42: +0.33	
Hand escape latency – friendly behaviour	–0.56	–0.88: –0.28	–0.04	–0.39: +0.42	*
Hand escape latency- aggression	0.16	–0.28: +0.47	–0.11	–0.40: +0.38	
Struggle behaviour–boldness	–0.08	–0.54: +0.20	0.07	–0.31: +0.54	
Struggle behaviour – friendly behaviour	0.10	–0.13: +0.53	–0.21	–0.73: +0.18	
Struggle behaviour–aggression	–0.25	–0.73: +0.15	0.01	–0.43: +0.39	
Boldness – friendly behaviour	0.75	+0.20: +0.87	–0.06	–0.35: +0.44	*
Boldness–aggression	–0.06	–0.64: +0.11	–0.05	–0.43: +0.54	
Friendly behaviour–aggression	–0.17	–0.73: +0.19	0.04	–0.58: +0.27	

Point estimates and accompanying credible intervals (CI) are shown. Asterisks in the ($P(\Delta r_{bi})$) column indicate whether males and females differ from each other based on overlap of credible intervals. Correlations with CIs not overlapping zero are displayed in bold.