



RESEARCH PAPER

Dimensions of Animal Personalities in Guinea Pigs

Benjamin Zipser*†, Sylvia Kaiser*† & Norbert Sachser*†

* Department of Behavioural Biology, University of Münster, Münster, Germany

† Otto Creutzfeldt Center for Cognitive and Behavioral Neuroscience, University of Münster, Münster, Germany

Correspondence

Benjamin Zipser, Department of Behavioural Biology, University of Münster, Badestrasse 13, 48149 Münster, Germany.
E-mail: Benjamin.Zipser@googlemail.com

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Abstract

Behavioural phenotypes can be studied from a variety of perspectives. Recent developments have focused on the individual, seeking patterns of behaviour that are stable over time and/or across different contexts (animal personalities). This study applied this method of understanding individual behavioural variability to domestic guinea pigs. Two behavioural domains were investigated: emotionality and social behaviour. Additionally, individual cortisol–stress reactivity and dominance status were examined. Adult male domestic guinea pigs living in large mixed-sex colonies were subjected to a series of behavioural and physiological tests twice with an intertest interval of 8 wk. Individual consistency over time was found regarding social behaviour, cortisol reactivity and dominance status, whereas no stability regarding emotional behaviour was detected. Furthermore, no stability over contexts was found. Our results suggest that the concept of animal personality is applicable to domestic guinea pigs. The ecological relevance of these data is underscored by the fact that they were obtained in animals from a very rich, socially complex scenario. Moreover, our study highlights that behaviour alone is not sufficient to describe individual phenotypic consistency. Physiological parameters such as stress reactivity should be included in animal personality research. Furthermore dominance – a relative measure which is not an absolute attribute of individuals – proved to be stable over time and thus also shed light on individuality.

Introduction

In its history, evolutionary biology has identified adaptive differences among ever smaller units of the taxonomic hierarchy. In recent years, this trend has peaked with the discovery that there are substantial adaptive differences even among single individuals of a social group (Wilson 1998; Dall et al. 2004). With regard to animal behaviour, such stable interindividual differences have been termed ‘temperament’, ‘animal personalities’ or ‘behavioural syndromes’. An ever increasing number of reports shows that animal personalities are widespread across a great variety of taxa such as fish, birds and mammals (Gosling 2001), and even non-vertebrates (e.g. Tremmel & Müller 2013) and theoretical models have investigated scenarios in which such

personalities can evolve (McElreath & Strimling 2006; Wolf et al. 2007).

There is no widely accepted standard definition yet, but most researchers agree that animal personalities are suites of correlated behaviours that result in consistent interindividual differences that are stable over time and/or across context (Sih et al. 2004; Réale et al. 2007). Yet, due to the novelty of the field, there are still conceptual and methodological difficulties (Carter et al. 2013), and thus, the specific way this concept is applied and interpreted varies greatly in the field. For example, the use of the two logical operators *and/or* shows that it is by no means clear whether both temporal *and* contextual stability of behaviour are necessary to constitute animal personality (Groothuis & Trillmich 2011). Moreover, with regard to temporal stability, it often is not specified over

which periods of time behaviour should be repeatable to be considered a stable personality trait. In fact, many authors argue that personalities should be more flexible over long timescales than currently assumed. This makes sense from a life-history point of view because environmental conditions and thus selection regimes on associations of behaviours might change throughout the lifespan of an individual (Bell et al. 2009; Réale et al. 2010; Stamps & Groothuis 2010; Sachser et al. 2013). However, studies investigating temporal stability of behaviour over extended periods of time are lacking (Réale et al. 2010), which might reflect the fact that it is harder to detect such effects as repeatability of behaviour tends to decrease with longer intertest intervals (Bell et al. 2009).

Furthermore, the definition of *context* is far from straightforward (e.g. compare Dingemans et al. 2010; Sih et al. 2004; Stamps & Groothuis 2010). Although most authors give very broad definitions of *context*, this is not always reflected in experimental data. In the early days of animal personality research, many studies focused on the so-called boldness–aggression activity syndrome, showing that animals which tend to explore unfamiliar environments more quickly also behave more aggressively towards conspecifics and are bolder towards predators (Huntingford 1976). Recent literature suggests investigating a wider spectrum of behavioural contexts such as mating behaviour, coping styles and cooperative behaviour (Sih & Bell 2008; Réale et al. 2010; Stamps & Groothuis 2010). Long-lasting correlations between very different contexts or the lack thereof might provide new insights into the structure of behavioural individuality.

This study sought to investigate putative animal personality traits in domestic guinea pigs (*Cavia aperea* f. *porcellus*) – a species in which no prior data concerning animal personality are available. Still, domestic guinea pigs are a well-suited model species to study animal personality as their complex social system is well understood (Sachser 1986a), and there is comprehensive knowledge about the way in which behavioural phenotypes can be shaped throughout the ontogeny of an individual. In several series of experiments, it has been shown that the social environment during critical phases in the ontogeny of an individual has an enduring impact on its behavioural and endocrinological profile (reviewed in Kaiser & Sachser 2005; Sachser et al. 2011). The social housing conditions in which the pregnant female lives have a gender-specific prenatal effect on offspring phenotype. Later in life, the social conditions during adolescence are critical for the further development of

individual traits of an animal – at least in males (Sachser 1993; Sachser & Renninger 1993; Sachser et al. 1994). For example, in contrast to males growing up in large mixed-sex colonies, males housed with a single female during adolescence show elevated levels of aggression, reduced levels of plasma testosterone and heightened hypothalamic–pituitary–adrenal (HPA) reactivity (Lürzel et al. 2010, 2011a,b).

However, studies – including those in guinea pigs – often compare groups of animals that have been differently treated or selected for different behaviours and kept in highly standardised stable conditions. This may bias results towards more behavioural consistency than would be found in more natural situations which are richer and more complex and therefore more likely to reshape behaviour. In our approach, we characterised the behavioural profiles of adult male guinea pigs living in large mixed-sex colonies in an individual-based approach. Colony housing provides animals with many social stimuli and thus complex social circumstances. Competition in such a scenario drives animals into specialised social roles such as ‘dominant’ or ‘subordinate’. In fact, it has been argued that the social environment and the resulting social niche specialisations are key factors for the evolution of personality (Bergmüller & Tabor-sky 2010).

We applied the definition of animal personalities as straightforward as possible and took some of the shortcomings in animal personality research into consideration for this study. For instance, studies investigating both, consistency over time and context are scarce: many do not test for repeatability over time at all (Gosling 2001). Furthermore, of those studies testing for consistency over time only very few (e.g. Guenther & Trillmich 2013) use test–retest intervals that account for a substantial percentage of the lifespan of the study species. Consequently, a long test–retest interval of 8 wk was chosen for this study. Furthermore, we investigated a broad spectrum of personality traits and thus different contexts. The two behavioural domains on which we focused were social and emotional behaviour. Cortisol–stress reactivity in a challenging situation was considered as a third domain of animal personalities. In addition to these three domains, we also analysed the dominance structure of the housing colonies, as the dominance status of an individual in a group has a vast impact on its behaviour and hormonal state (Sachser 1986a; Sachser & Pröve 1986; Sachser et al. 1998).

In accordance with the definition of personality, we hypothesise that guinea pigs show individual stability over time in these three domains and that these

domains represent different contexts across which individual consistencies can be found.

Animals, Materials and Methods

Animal Husbandry

The animals used for this study were male descendants of the heterogeneous short-haired and multi-coloured breeding stock of domestic guinea pigs (*Cavia aperea* f. *porcellus*) of the Department of Behavioural Biology at the University of Münster. They stemmed from four colony housing groups (A–D) that are maintained there. Group A and B were established from 40 founder animals obtained from a professional breeder in 1975. To counteract inbreeding, individuals from other breeders were cross-bred into the stock sporadically since then. Group C and D were established from various founder animals obtained from several professional breeders in 2010. Group A and B were housed in one breeding room and group C and D in another room. The animals showed a graduated age structure ranging from 1 to 19 mo and were composed of 12–15 females, 8–10 males and their offspring. As soon as an animal reached 19 mo of age, it was taken from the colony, and an offspring of the same sex was allowed to grow up. These animals replaced the one removed from the colony to keep the number of individuals in the colony constant. Replacement females remained in their birth colony, whereas replacement males were transferred to the neighbouring colony in the same breeding room at their 30th day of age. All other offspring not used to replace an old animal were removed from the colonies at about 21 d of age. Each colony was housed in a wooden enclosure (6 m²) that contained three wooden shelters, a centrally located food pan and 6–7 water bottles. All individuals could be identified by natural markings and were housed under controlled conditions: 12:12 L/D (lights on at 07:00 a.m.), temperature 20 ± 2°C and relative humidity 50% ± 10%. Commercial guinea pig diet, which contains all relevant nutrients for guinea pigs (Höveler 'Spezialfutter' 1070 for guinea pigs, Höveler Spezialfutterwerke GmbH & Co. KG, Langenfeld, Germany), and tap water were available *ad libitum*. Every week, this diet was supplemented once with straw and six times with hay. Vitamin C was provided in the water twice per week. The floors were covered with wood shavings. Cleaning of enclosures occurred weekly. All experiments were announced to the local authorities and were approved by the 'Tierschutzbeauftragter' of the

University of Münster (Reference number: 8.87-51.05.20.10.263).

Experimental Design

Animals were subjected to a first series of behavioural tests including (in order of completion) an open-field test (OF), a dark–light test (DL), a step-down test (SD), a male/female interaction test (MF) and a cortisol reactivity test (CR) after reaching an age of at least 6 mo in their home colony. At this age, colony-housed males can reach a social status that allows them to successfully defend and mate with females for the first time (Sachser 1986a). This was carried out as we were interested in personalities of fully adult individuals.

At the beginning of the first series of tests, the animals' age ranged from 209 to 520 d (322 d average). All tests were completed within a maximum of 13 d with a maximum of 5 d between two subsequent tests and a maximum of one test per day. Behavioural testing took place between 12:30 h and 15:15 h. The housing room of the subjects was not entered 30 min prior to behavioural tests and 60 min prior to the CR. Experiments were split into four blocks, each block comprising all fully adult males stemming from the same housing colony. Four to six individuals from each colony fell into that category resulting in a total of 19 experimental animals. Data in some tests could not be acquired for all animals due to illnesses. These animals were excluded from the study, which reduced sample sizes in the final analyses (see Data Analysis and Statistics).

Within ten days after the last animal of the same housing colony had completed its CR, the dominance hierarchy of the males of the corresponding colony was assessed on five subsequent days. All males of the group were included in the dominance evaluation. Observation bouts lasted from 30 to 120 min and took place between 09:00 h and 18:30 h with a total daily observation time of 4 h. This added up to a total observation time of 20 h per group, equally distributed among animals in a pseudo-randomised recording schedule. Focal group sampling and continuous recording were used, with a maximum of four individuals per focal group (Martin & Bateson 1993). The experimenter was present in the room for live observation. As four different colonies were investigated, dominance ranks could not be compared directly between animals stemming from different colonies. Hence, the Coulon Index of each experimental animal from each colony was calculated to compare dominance across colonies. This widely used index is

defined as the number of won agonistic interactions divided by the number of all agonistic interactions in which the subject was involved (Coulon 1975). In guinea pigs, the most reliable indicator to determine whether an agonistic interaction is won by the focal animal is the retreat of the opponent in an agonistic encounter. Hence, an interaction was scored as 'won' if the opponent showed a directed movement to a location at least one body length away from the focal animal. This retreat had to occur within 3 s after an agonistic behaviour pattern or an approach (closer than one body length) of either of the individuals. For a detailed description of the agonistic behavioural patterns see Kunkel & Kunkel (1964), Rood (1972) and Sachser (1986a,b).

Fifty-four to fifty-nine days after the first animal of one housing colony had experienced the OF, the testing series and the recording of the dominance hierarchy were repeated in the same manner as before. The animals' age ranged from 265 to 576 d (375 d average) when entering the second experimental phase. This time span between testing series accounts for about 2.8% of the 6 yr average life expectancy of a male domestic guinea pig (Kaiser et al. 2010). At first glance, this may not appear as much, but transferred to an average life expectancy of about 69 yr in humans (WHO 2009), it would amount to approximately 2 yr which is a common interval in studies on human personality psychology (Schuerger et al. 1989; Roberts & DelVecchio 2000).

Behavioural Tests and Cortisol-Reactivity Test

All tests were conducted in a wooden enclosure of 1 × 1 m size with a wall height of 50 cm. For subsequent analysis all behavioural tests, except for the SD and the CR, were videotaped. Except for the SD, the experimenter was not present in the room during testing. Testing took place in a guinea pig housing room other than the animals' home colony room. Animals were caught in their home colony, put into an empty standard Makrolon cage type III and subsequently transported to the testing room. Behavioural tests lasted 15 min, except for the SD, which lasted 7 min. Behavioural scoring was performed using focal animal sampling and continuous recording (Martin & Bateson 1993).

Tests on emotionality

Regarding emotional behaviour, we adapted short behavioural tests that are commonly used to

characterise emotional behaviour in mice and rats for guinea pigs.

Open-field test. The 1 × 1 m test enclosure constituted the OF. Soiled bedding from the animal's home colony was mixed with clean bedding and scattered on the floor to reduce the novelty of the experimental setting. Animals were placed into the centre of the experimental enclosure. For analysis of explorative behaviour, the enclosure was subdivided into 16 equal virtual squares (25 × 25 cm). The four inner squares were defined as the centre of the OF. Parameters recorded were as follows: *virtual squares crossed per time* as a measure of exploration and *percentage of time spent in the central area* as a measure of anxiety-like behaviour (Crawley et al. 1997; Holmes 2001).

Dark-light test. For the DL, soiled bedding from the animal's home colony was mixed with clean bedding and scattered on the floor to reduce the novelty of the experimental setting. The wooden dark-light box (300 mm width, 265 mm height and 250 mm depth) was put at the midpoint of one of the enclosure's walls. The top of the box could be opened for placement of the subject. The front of the box had a 150 × 300 mm door. The animals were placed into the closed dark-light box where they were allowed to acclimate for 60 s. Then, the front door was opened to allow the animal to explore the enclosure. Parameters recorded were as follows: *Latency to leave the dark box* and *time spent in the light area* as measures of anxiety-like behaviour as well as *number of times the animal entered the light area* as indicator of exploration (Hascoët et al. 2001). Entering the enclosure was defined as the time point at which the animal completely moved out of the dark box into the enclosure.

Step-down test. The SD tower was put in the centre of the enclosure, parallel to the walls. The floor of the enclosure was covered with fresh wood shavings. The tower had a base area of 300 × 300 mm and a height of 235 mm. The platform was covered with fresh wood shavings. Mounted 235 mm above the platform was a roof (300 × 300 mm). The transport cage was put on the floor of the experimental room, and the animal was allowed to acclimate for 60 s. Subsequently, it was placed on the platform facing one of the four edges. The animal was gently held still until its reflex to escape the experimenter ceased. The subject was then released, the experimenter stepped aside and the *latency to step down* the platform was measured as a measure of risk-taking. It was defined as the time point at which the animal

touched the floor of the enclosure with all four paws.

Social behaviour

Male/Female interaction. For the MF the enclosure was divided into two equal halves with a wooden board. The floor was covered with fresh wood shavings. An unfamiliar female was put into one half. These females had given birth at least once, were pregnant and not due to give birth for the upcoming 2 wk. Hence, the females were never in oestrus during the experiments. The experimental animal was put in the other half of the enclosure. After an acclimation period of 60 s, the dividing wall was removed and the animals could explore each other. Behavioural patterns recorded were as follows: *courtship behaviour* (*intensive anogenital licking*: subject lowers and turns its head and touches, sniffs, licks and/or nuzzles the anogenital region of the female; and *rumba*: subject rhythmically oscillates its hind quarters from side to side); *sexual behaviour* (*mounting*: subject places at least the front third of its body over the hindquarters of the female's body – typically includes clasping the flanks of the female with the forepaws; and *pelvic thrust*: while *mounted*, the animal rhythmically moves its hindquarters back and forth). All of these behaviours were scored as frequencies. Furthermore, the *latency to show sexual or courtship behaviour* and the *latency to mount* were recorded. The behavioural definitions used are derived from previous studies on sexual and courtship behaviour in male domestic guinea pigs (Kunkel & Kunkel 1964; Rood 1972; Sachser 1986a). For the first series of MF tests, two females from a colony other than the subjects' home colony were chosen and confronted to all the subjects from that particular series. No female was used more than once a day. In the second series, two different females were chosen as partners (again from a colony other than the home colony). Thus, the subjects were never tested with the same female in the first and second trial.

Cortisol-Reactivity Test

Animals were placed into the centre of the enclosure that contained food and water *ad libitum* for 2 h. The floor was covered with fresh wood shavings. A novel environment has been shown to act as a psychological stressor in guinea pigs, causing an increase in cortisol (C) levels (Hennessy et al. 2006). All tests were started at 13:00 h \pm 15 min. This time was chosen as

domestic guinea pigs show diurnal variations in plasma C titres with a reliable peak around 13:00 h (Sachser 1994). At the beginning of each test, the animal was caught from its home enclosure and a blood sample was taken to assess initial C concentrations. After that, the animal was introduced into the unfamiliar environment. At 60 min (reaction value 1, R1) and 120 min (reaction value 2, R2), subsequent blood samples were taken to determine changes in C concentrations. After the third blood sample, the animal was placed back into its home enclosure. The parameters evaluated were as follows: *initial C concentration* (I), R1, R2, *maximal reaction value* (MAX), *absolute C increase from I to R1*, *absolute C increase from I to R2*, *absolute C increase from I to MAX*.

Blood samples were collected from the blood vessels of the ears. A muscle salve (Elacur hot, Riemser Arzneimittel AG, Greifswald – Insel Riems, Germany) was applied to the ear to stimulate circulation, and the vessels were illuminated with a cold light lamp. Vessels were pricked with an injection needle and about 0.4 ml of blood was collected in heparinised capillary tubes. One experimenter held the animal in his/her lap, while a second collected the sample. Guinea pigs show little struggling during the collection procedure, and no elevation of plasma C occurs for about 5 min (Sachser 1994). Accordingly, all samples for determination of C levels were collected within 3 min of entering the room to make sure that no elevation of C had yet occurred. Because no anaesthesia is required, hormone levels in the second and third samples were not influenced by previous exposure to anaesthesia. Plasma was separated by centrifugation (11 700 \times g for 5 min) and deep-frozen (-20°C) until assayed.

Plasma C concentrations were determined using a luminescence enzyme-linked immunosorbent assay (ELISA; Cortisol ELISA Kit, IBL International GmbH, Hamburg, Germany). The antibody used cross-reacted with relevant steroids as follows: prednisolone 29.8%, 11-desoxycortisol 8.48%, cortisone 4.49%, prednisone 2.12%, corticosterone 1.99%, 6 β -hydroxycortisol 1.03%. The intra-assay% CV was 3.2%, the interassay% CV was 6.1%.

Data Analysis and Statistics

Videotapes were digitised and subsequently evaluated using the behavioural observation and analysis programme *The Observer XT* (Version 8, Noldus Information Technology, Wageningen, the Netherlands).

All data were tested for normal distribution by descriptive analysis of histograms and application of

the one sample Kolmogorov–Smirnov test. In cases in which criteria for normal distribution were not met the corresponding data set was transformed (\log_{10}) to achieve normal distribution. This was the case for *time spent in the open field* (DL, first testing series), *rumba* and *mounting* (MF, second testing series). If this still did not result in normally distributed data, nonparametric statistics were used. This was the case for the following variables: *latency to step down* (SD, both testing series) and *pelvic thrust* (MF, both testing series).

For correlational analyses, Pearson product-moment correlations were used for normally distributed data, whereas Spearman's rank correlations were used for non-normally distributed data.

Bivariate cross-correlations between tests were carried out using only one variable of each test. The variables chosen were those that best reflected the main purpose of the test. The OF is a paradigm which is mainly based on locomotor activity which reflects exploration (Lister 1990). Hence, the *number of virtual squares crossed* was chosen in this test. The DL test was developed to investigate anxiety-like behaviour (Lister 1990). The *time spent in the light compartment* of the dark–light apparatus was thus chosen as it is widely accepted as reliably reflecting anxiety-like behaviour in mice and other rodents (Hascoët et al. 2001). In the SD test, the *latency to step down* was the only variable and thus was used to represent the test. Regarding MF interaction test, the *frequency of courtship behaviour* was selected as all (but one) males showed courtship behaviour in contrast to sexual behaviour, which was only shown by approximately half of the individuals. The CR measures the psychological stress induced by a novel environment. The *increase from initial value to the maximal reaction value* was chosen as representative variable. Finally, dominance rank in the home colony was investigated using the Coulon Index, and consequently, this parameter was also incorporated in the cross-correlational analyses. This made it possible to assess whether dominance in the colony is related to behaviour or cortisol reactivity in the tests conducted.

To control for possible habituation effects, comparisons of means over time were calculated. Comparisons of means of two related samples were made using the paired *t*-test (normally distributed data) or the Wilcoxon matched-pairs signed-ranks test (not normally distributed data).

All calculations were performed two-tailed. For all tests, a significance level (α) of 0.05 was selected. All tests were calculated using the software package SPSS Statistics 13.0 (SPSS Inc.).

The final sample sizes and colony compositions of experimental animals were as follows: results in which $n = 15$ are based on four animals from colony A, B and C and three animals from D; for $n = 14$ the composition was: four A and B three C and D; for $n = 13$ (two subsamples used) the compositions were: either four A and B, three C, two D; or three A, C and D, four B.

Results

Stability of Behaviour and Cortisol Reactivity over Time

Emotionality

Concerning stability of behaviour over time, neither *squares crossed per minute* ($r = 0.015$, $p \leq 0.958$, $n = 15$) nor *percentage of time spent in the centre of the open field* ($r = -0.045$, $p \leq 0.875$, $n = 15$) significantly autocorrelated in the OF. Similarly, in the DL, none of the measured behavioural patterns were autocorrelated over time: *latency to leave the dark box* ($r = 0.311$, $p \leq 0.259$, $n = 15$), *number of times the animal entered the light area* ($r = 0.336$, $p \leq 0.221$, $n = 15$) and *time spent in the light area* ($r = 0.364$, $p \leq 0.244$, $n = 15$). Finally in the SD, the *latency to step down* from the tower was not repeatable over time ($r_s = -0.191$, $p \leq 0.495$, $n = 15$). Hence, over the course of the 8-wk span between testing phases, no stability of emotional behaviour (exploration, anxiety-like behaviour, risk-taking) could be found.

Concerning changes of group means over the 8-wk testing period, only one of the six measures of emotional behaviour was affected. *Squares crossed per minute* (OF) significantly decreased over time ($\bar{x} \pm \text{SEM}$): 5.6 ± 0.74 vs. 3.6 ± 0.57 ; $T = 2.2$, $p \leq 0.044$, $n = 15$. No such changes of means over time were found regarding all other variables of emotionality (for all comparisons, $n = 15$ and $p \geq 0.1$): OF *percentage of time spent in the centre of the open field* (14.1 ± 5.4 vs. 16.9 ± 6.0 ; $T = -0.351$), DL *latency to leave the dark box* (s) (546.0 ± 101.7 vs. 419.5 ± 107.0 ; $T = 1.03$), DL *number of times the animal entered the light area* (0.87 ± 0.24 vs. 1.53 ± 0.42 ; $T = -1.63$), DL *time spent in the light area* (s) (125.1 ± 69.1 vs. 79.8 ± 25.5 ; $Z = -0.45$), SD *latency to step down* (s) (213.0 ± 52.4 vs. 272.4 ± 50.5 ; $Z = -0.98$).

Social behaviour

Male/Female Interaction. Stability over time was clearly found regarding male/female interactions. A positive correlation was found for *latency to show sexual or court-*

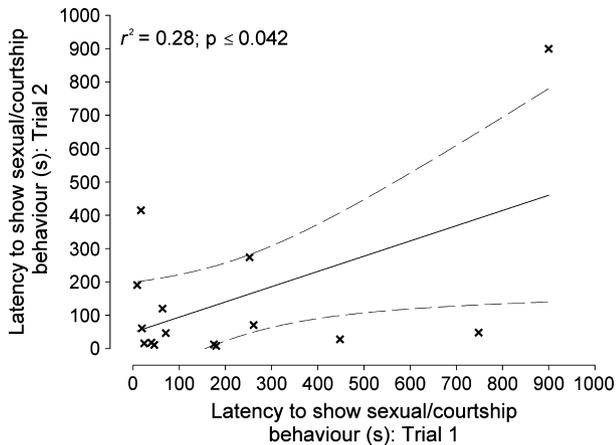


Fig. 1: Correlation over time (8 wk). Latency of sexual or courtship behaviour (intensive anogenital licking, rumba, mounting, pelvic thrust) when exposed to an unfamiliar female. 'X's represent single individuals ($n = 15$). Pearson's product-moment correlation analysis revealed a significant correlation between the trials explaining 28% of the variance. The 95% confidence interval (dashed lines) is also shown.

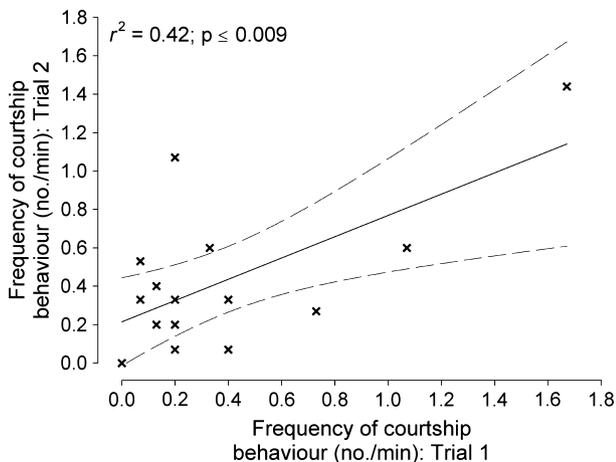


Fig. 2: Correlation over time (8 wk). Frequency of courtship behaviour (intensive anogenital licking and rumba) shown when exposed to an unfamiliar female. 'X's represent single individuals ($n = 15$). Pearson's product-moment correlation analysis revealed a significant correlation between the trials explaining 42% of the variance. The 95% confidence interval (dashed lines) is also shown.

ship behaviour ($r = 0.531$, $p \leq 0.042$, $n = 15$, Fig. 1). Males that initiated sexual and courtship behaviour early during the first testing phase did so in the second phase as well (Fig. 1). Moreover, frequency of courtship behaviour (intensive anogenital licking plus rumba) was also highly consistent over time ($r = 0.645$, $p \leq 0.009$, $n = 15$, Fig. 2). Individuals that engaged in frequent courtship behaviour in the first testing phase also showed a high frequency of courtship behaviour in

the second testing period. Positive correlations over time also were obtained for individual courtship patterns: *intensive anogenital licking* ($r = 0.615$, $p \leq 0.015$, $n = 15$), *rumba* ($r = 0.703$, $p \leq 0.003$, $n = 15$). In contrast, sexual behaviour was not consistent over time: *mounting* ($r = -0.122$, $p \leq 0.666$, $n = 15$), *pelvic thrust* ($r_s = -0.196$, $p \leq 0.483$, $n = 15$), *latency to mount* ($r = 0.094$, $p \leq 0.739$, $n = 15$).

Cortisol reactivity

The initial plasma cortisol concentrations (I) did not change significantly over time ($\bar{x} \pm \text{SEM}$; ng/ml): 145.3 ± 38.8 vs. 242.2 ± 60.7 ; $T = -0.352$, $p \leq 0.731$, $n = 14$. These initial values were also not individually consistent over time ($r = 0.64$, $p \leq 0.829$, $n = 14$). However, all parameters representing cortisol reactivity showed highly significant (positive) temporal correlations. The reaction values R1 (after 1 h) and R2 (after 2 h) were stable over time (R1: $r = 0.686$, $p \leq 0.01$, $n = 13$; R2: $r = 0.797$, $p \leq 0.001$, $n = 13$). Also, the maximal reaction value reached by an animal during the test (R1 or R2) was stable over time ($r = 0.730$, $p \leq 0.005$, $n = 13$). Furthermore, the absolute increase in plasma cortisol from I to R1 showed a positive correlation over time ($r = 0.62$, $p \leq 0.024$, $n = 13$) as well as the absolute increase from I to R2 ($r = 0.776$, $p \leq 0.002$, $n = 13$). Finally, maximal cortisol increase (I to MAX) in phase one was positively associated with the maximum response in testing phase two, 8 wk later ($r = 0.720$, $p \leq 0.005$, $n = 13$, Fig. 3). In summary, cortisol reactivity proved as a highly stable trait over the course of the experiment.

Dominance rank in the home colony

The dominance rank index in the home colony (Coulon Index) was significantly correlated over time ($r = 0.527$, $p \leq 0.043$, $n = 15$, Fig. 4). Males held their relative dominance positions in their home colonies over the 8-wk period between testing phases.

Correlation of Behavioural Parameters and Cortisol Reactivity across Context

To look for consistencies between different contexts, cross-correlations of parameters from the three domains of emotionality, social behaviour and cortisol reactivity as well as the dominance rank index were calculated in both testing phases. This resulted in 36 cross-correlations, none of which were signifi-

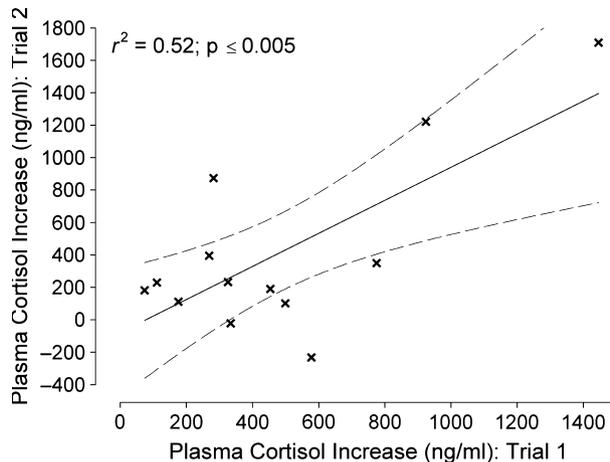


Fig. 3: Correlation over time (8 wk). Plasma cortisol response after exposure to a psychogenic stressor (cortisol-reactivity test: initial value to maximal reaction value). 'X's represent single individuals ($n = 13$). Pearson's product-moment correlation analysis revealed a significant correlation between the trials explaining 52% of the variance. The 95% confidence interval (dashed lines) is also shown.

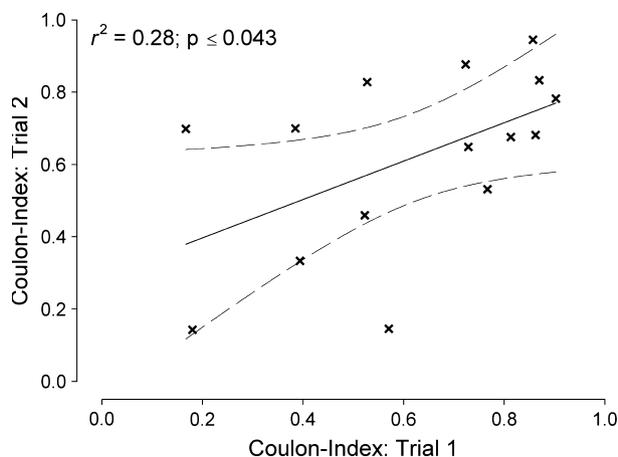


Fig. 4: Correlation over time (8 wk). Dominance rank indices in the home colony (Coulon Index). 'X's represent single individuals ($n = 15$). Pearson's product-moment correlation analysis revealed a significant correlation between the trials explaining 28% of the variance. The 95% confidence interval (dashed lines) is also shown.

cant in neither of the two testing series. The three emotionality parameters (from OF, DL, and SD) were neither correlated among each other nor correlated with any parameter of the other two domains (social behaviour and cortisol reactivity). Furthermore, social behaviour and cortisol reactivity also were not correlated. Finally, none of the parameters from all three domains were correlated with the rank index, and thus, there was no apparent association of dominance in the home colony and performance in the tests.

Discussion

Stability of Behaviour and Cortisol–Stress Reactivity over Time

Emotionality

None of the parameters investigated in the tests of emotional behaviour were repeatable over time. Two alternative conclusions could be drawn from these results: either the tests did not capture the emotional behaviour correctly or temporal stability of emotional behaviour is simply not present in colony-housed adult male guinea pigs. We prefer the second alternative for the following reasons. First, habituation can make it harder to detect stability of behavioural responses over time as prior experience can alter the reaction to personality tests (Frost et al. 2007). In the present study, however, this possibility is highly unlikely as only one of the six investigated variables representing emotionality showed a significant decrease over time. Second, in the ancestral form of the domestic guinea pig – the wild cavy (*Cavia aperea*) (Künzl et al. 2003) – stability of emotional behaviour has been found (Guenther & Trillmich 2013) using an experimental paradigm comparable with the one used here. On the one hand, this could mean that the test applied in the aforementioned study is only suitable for wild cavy and not domestic guinea pigs. On the other hand, it suggests an intriguing hypothesis: The lack of temporal stability of emotional behaviours in guinea pigs might be a result of domestication. If this is the case, the question arises why stability of emotional traits is relevant for cavy but not for domestic guinea pigs.

Many current theories on the emergence of personality traits are based on the premise that the environment can be highly unpredictable (Dall et al. 2004; Sih et al. 2004; McElreath & Strimling 2006). In highly uncertain, ever-changing environments a high degree of flexibility would mean that individuals would have to change their behavioural responses constantly according to the changes in the environment. This costly investment in a changed behavioural response profile, however, runs a high risk of not paying off as the environment might already have changed again which would render the made behavioural changes useless. In such situations, it pays to develop stable suites of behavioural responses that do best in most situations, although this brings the risk of behaving inappropriately in some (Dall et al. 2004; Sih et al. 2004; McElreath & Strimling 2006). This argument can be applied to the different situations of wild cavy and domestic guinea pigs. In

the natural habitat of wild cavies, the environment can be highly unpredictable. Natural factors such as predation pressure lead to tremendous fluctuations regarding population density (Asher et al. 2004, 2008). Differences in population density in turn have an impact on intraspecific competition for resources such as shelter or food (Kaiser & Sachser 2005). Thus, it might be the case that stable personality traits are valuable for wild cavies, especially regarding emotionality. At times of high predation pressure, it might pay to be highly cautious, less explorative and less risk-prone, whereas in less dangerous times, the opposite might be advantageous. One of the central characteristics of domestication is removal of exactly these unpredictable environmental influences (Price 1984). By removing these selection pressures during domestication, stable emotional responses might have become obsolete and thus vanished in domestic guinea pigs.

Social behaviour

With regard to sexual and courtship behaviour, a clear consistency over time was found. In classical studies on guinea pigs, similar consistencies were obtained. Male guinea pigs were exposed to an unfamiliar oestrus female, and their sexual and courtship behaviour was scored resulting in individual males' 'sex drive'. This drive proved to be individually stable over long periods (weeks/months) of time (Young & Grunt 1951; Grunt & Young 1953). The authors further classified males into 'low', 'medium' and 'high'-drive individuals. After castration and cessation of sexual behaviour, experimental androgen replacement re-induced sexual behaviour with individuals returning to their respective groups of 'sex drive' (Grunt & Young 1953). The present study is in line with this pioneering work and additionally shows stability of sexual and courtship behaviour on an individual level.

Our data show that the amount of sexual and courtship behaviour shown in both testing phases was not correlated with dominance rank in the home colony. This might come as a surprise because social dominance is generally thought to result in priority of access to resources such as mates and ultimately to a higher reproductive success (Drews 1993; Ellis 1995; Sachser et al. 1998). In colony-housed guinea pigs, high ranking males have priority of access to the receptive females and defend their mating partners, especially during oestrus (Sachser 1986a; Sachser et al. 1998). Consequently, the rank of an individual is positively correlated with the amount of sexual and

courtship behaviour shown in the colony (Sachser 1986a; Sachser & Pröve 1986). However, in the present study, no other males were present while the individuals interacted with the female. Subdominant individuals may thus have displayed the amount of sexual and courtship behaviour they would have shown in the colony if they were not prevented from doing so by dominants. The presence of other males might override the personality trait. Interestingly, a similar social phenomenon in guinea pigs has been shown for agonistic behaviour. Adult colony-housed males of different dominance status were taken out of their home group and presented singly with a strange male conspecific. The dominance rank of the male in its home group did not predict its agonistic behaviour in the pairwise interaction (Sachser 1987).

In conclusion, this trait can be interpreted as an intrinsic tendency to show sexual and courtship behaviour when not influenced by other social stimuli.

Cortisol–stress reactivity

Perhaps the most striking result of our study is the strong repeatability of cortisol–stress reactivity. A wide variety of different measures of this trait proved to be stable over time demonstrating the robustness of this result (e.g. increase from initial value to reaction value 1 or 2, increase from initial value to maximal reaction value). To our knowledge, our study is among the few to ever show such an individually stable cortisol response pattern over time. For example, research on tree shrews showed a highly stable pattern of cortisol reactivity over several months (Von Holst 1998) when animals were kept under constant, highly standardised conditions. By contrast, our data show that patterns of cortisol–stress reactivity can also be individually stable over long periods of time in a very complex and rich social environment.

There is also a crucial difference between our results and research reporting temporally stable patterns of stress reactivity in the animal personality literature (Carere et al. 2010): The majority of these data stem from studies pre-classifying or even preselecting for contrasting behavioural profiles which in turn are associated with specific neuroendocrinological patterns. The proactive and reactive coping styles in mice and rats are probably the most prominent example of this phenomenon (Koolhaas et al. 1999; Carere et al. 2010). Stable stress-reactivity profiles have also been found in domestic guinea pigs before, but only by comparing differently treated groups of individuals. For example, guinea pig males housed with a single

female during adolescence show elevated levels of aggression, reduced levels of plasma testosterone and a high HPA reactivity, in comparison with males that were raised in a colony (Lürzel et al. 2010, 2011a,b).

As with sexual and courtship behaviour, no correlation of cortisol reactivity with dominance in the home colony was found. This, however, was not surprising. A huge body of evidence in many different species clearly shows that the dominance status of an individual does not directly predict its level of HPA activity (e.g. reviewed in: Sapolsky 2005). There are cases in which dominants are the least stressed individuals of a group but the opposite can also be the case. This also holds true for male domestic guinea pigs, in which low hierarchy positions do not necessarily lead to enhanced stress responses (Sachser et al. 1998).

Correlation of behavioural parameters and cortisol-reactivity across contexts

Surprisingly, no cross-correlations among the three domains of emotionality, social behaviour and cortisol reactivity were found during either of the two testing phases meaning that stability of behaviour and stress reactivity across contexts was not detectable – at least with the definition of context used here. Emotionality, social behaviour and stress reactivity were chosen to represent major dimensions of animal personalities that represent different contexts. However, this does not necessarily mean that correlations across different contexts do not exist in domestic guinea pigs in general. It is possible that correlations of personality traits across context do only occur during specific phases of ontogeny, only in certain populations of individuals or only in certain environmental situations (Sih et al. 2004; Bell & Sih 2007). In sticklebacks, for example, it was shown that a single 24-h exposure to a predator induces a stable correlation between boldness and aggression that was not present in the sample before the exposure (Bell & Sih 2007). As contextual correlations in animal personalities can be so volatile, we argue that the lack of cross-context correlations in the data is no reason to reject the hypothesis that animal personalities exist in domestic guinea pigs. Moreover, the definition used here, and by others (e.g. Réale et al. 2007), asserts that either temporal *or* contextual consistency is sufficient to speak of animal personalities.

Conclusions

Four main conclusions emerge from our results. First, we add the domestic guinea pig to the ever-

growing number of species showing animal personality traits.

Second, no consistency over time was found regarding emotionality. However, repeatability in this behavioural domain was shown in wild cavies (Guenther & Trillmich 2013). We thus hypothesise that the lack of stability in the domestic form was brought about by changing selection pressures during domestication.

Third, besides behaviour, we expanded the idea of putative animal personality traits to the physiological parameter of cortisol–stress reactivity. As this trait was highly stable over time and the HPA axis is one of the fundamental physiological systems animals need to cope with challenge, we suggest that it is crucial to include this parameter into animal personality research. Indeed, it has been shown in several mammalian and avian species that individual differences in stress physiology are often tightly linked to specific behavioural personality profiles as in the proactive/reactive coping style model (reviewed in Carere et al. 2010).

Fourth, none of the temporally stable traits was correlated with dominance – a third trait that was repeatable over time. Consequently, it can be concluded that the stability of sexual and courtship behaviour and cortisol reactivity represent genuine personality traits and not simply a secondary attribute conveyed by the respective dominance rank of an individual. Still, dominance rank is highly important for individuals including guinea pigs as it conveys social roles, limits the amount of escalated aggression in a group and structures the individual access to resources (Sachser 1986a; Sachser & Pröve 1986; Ellis 1995; Sachser et al. 1998). Some authors argue that dominance can be a personality domain itself, whereas we prefer to treat it as a separate entity, as has been argued before (see reviews: Freeman & Gosling 2010; Gosling & John 1999). From this point of view, dominance status is regarded as a social outcome determined by a variety of factors including personality, physical traits and specific social situations. By that reasoning, ‘aggressiveness’ could be a putative personality trait, but not dominance, which is a relative measure resulting from repeated agonistic interactions between individuals and consequently not an absolute property of a single individual (Drews 1993). We thus suggest that in addition to behavioural and physiological personality traits, dominance status of individuals should be investigated to comprehensively describe individual behavioural phenotypes.

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