

Domestication effects on behavioural traits and learning performance: comparing wild cavies to guinea pigs

Vera Brust · Anja Guenther

Received: 5 January 2014 / Revised: 4 June 2014 / Accepted: 25 June 2014
© Springer-Verlag Berlin Heidelberg 2014

Abstract The domestication process leads to a change in behavioural traits, usually towards individuals that are less attentive to changes in their environment and less aggressive. Empirical evidence for a difference in cognitive performance, however, is scarce. Recently, a functional linkage between an individual's behaviour and cognitive performance has been proposed in the framework of animal personalities via a shared risk–reward trade-off. Following this assumption, bolder and more aggressive animals (usually the wild form) should learn faster. Differences in behaviour may arise during ontogeny due to individual experiences or represent adaptations that occurred over the course of evolution. Both might singly or taken together account for differences in cognitive performance between wild and domestic lineages. To test for such possible linkages, we compared wild cavies and domestic guinea pigs, both kept in a university stock for more than 30 years under highly comparable conditions. Animals were tested in three behavioural tests as well as for initial and reversal learning performance. Guinea pigs were less bold and aggressive than their wild congeners, but learnt an association faster. Additionally, the personality structure was altered during the domestication process. The most likely explanation for these findings is that a shift in behavioural traits and their connectivity led to an altered cognitive performance. A functional linkage between behavioural and cognitive traits seems to exist in the proposed way only under natural selection, but not in animals that have been selected artificially over centuries.

Keywords Personality · Cognition · Reversal learning · Domestication · Cavy

Introduction

The process of domestication is well known to cause behavioural and morphological differences in animals in relation to their closest wild relatives (e.g. Clutton-Brock 1989; Jensen 2006; Plyusnina et al. 2011). Implications on cognitive abilities, however, are less well documented (Harker and Whishaw 2002; Range et al. 2012) although they have moved into the focus of attention in the last couple of years (e.g. Lindqvist and Jensen 2009; Lewejohann et al. 2010; Albiach-Serrano et al. 2012). During the process of domestication, animals need to adapt to the human presence and usually comparatively small-scaled habitats (Hediger 1964; Price 1984). At the same time, the absence of non-human predation as well as constant group composition and nutritional supply offer a high level of environmental stability (Kruska and Steffen 2013). The resulting artificial environments provide unnaturally low risk conditions (Price 1999). Early life experiences are especially well known to shape an adult individual's behavioural phenotype (West-Eberhard 2003; Koolhaas et al. 2006; Del Giudice 2012), hence such low risk conditions in general lead to individuals that are less responsive to changes in their environment (Künzli and Sachser 1999; Price 1999) and show less predation avoidance (Price and Huck 1976; Klefoth et al. 2012). Combined with selective breeding, these effects can become even more pronounced over the course of the domestication process (Price 1999). In a similar fashion, encounters with conspecifics increase when individuals are kept together in unnaturally high numbers without the possibility to

V. Brust (✉) · A. Guenther
Department of Animal Behaviour, Bielefeld University,
Morgenbreede 45, 33615 Bielefeld, Germany
e-mail: vera.brust@uni-bielefeld.de

disperse (Kruska and Steffen 2013). Consequently, domestic phenotypes behave less aggressive as again favoured by both, early development and human selection (e.g. Price and Huck 1976; Plyusnina et al. 2011). Taken together, the altered combination of environmental factors causes changes in the behaviour of domesticated forms towards less attentive, cautious and aggressive individuals.

Individual differences in behaviour within species, often referred to as animal personalities, occur frequently throughout the animal kingdom (Réale and Dingemanse 2001; Sih et al. 2004a, b). Domestic individuals should represent extreme phenotypes of the behavioural spectrum within their species due to artificially induced directed selection towards specific behavioural traits, e.g. tameness or social compatibility (Huntingford 2004). Sih and Del Giudice (2012) recently reviewed evidence for a functional linkage between behavioural traits and cognitive performance via a shared underlying risk–reward trade-off that is present in many behaviours: Individuals with risk-prone behavioural types (i.e. bold and/or aggressive) should be fast and thus more successful in gathering resources over the short term, but at the same time face a high mortality risk. Animals with risk-averse behavioural types (i.e. shy and/or passive), however, should be slow and careful and consequently sacrifice short term gains more frequently, but live more safely. Additionally, risk-prone behavioural types should be linked to a fast cognitive style, including traits such as learning fast and forming routines readily, while a risk-averse behavioural type is often associated with slow learning and at the same time remaining behaviourally flexible. Being of a fast or slow behavioural and cognitive type at the same time might consequently be functionally related in order to represent a fast, risk-prone or, respectively, slow and risk-averse phenotype.

Following the idea of such a linkage between behavioural and cognitive traits, wild animals should differ from their domestic congeners not only in behavioural traits, but also in cognitive performance. However, a linkage between behavioural and cognitive traits is not the only possible explanation for differences in cognitive performance between lineages. The brain of domestic mammals is usually smaller compared with their wild forms (Jensen 2006). In guinea pigs, the braincase volume is reduced by 16.2 % when compared with wild cavies of the same body size (Kruska and Steffen 2013). Generally, behavioural complexity seems to increase with brain size. However, linking brain size to cognitive ability is not as straight forward as it seems, as it does not take differences in composition and function into account and thus may not give much evidence for actual differences in cognitive performance, see Aboitiz (1996) and Healy and Rowe (2007) for reviews.

Just as differences in brain size arose from differences between natural and artificial selection, cognitive traits

may face different selection pressures in domesticated and wild congeners. Wild animals may be under selection pressure for cognitive skills like learning where to find food and memorizing its location (Lindqvist and Jensen 2009). This selection should be relaxed under domestic conditions where food is usually highly abundant and provided in stable patterns with regard to time and space (Frank 1980). Besides being less cognitively challenging, the physical environment in captivity is generally simpler and more predictable compared to the natural habitat (Kruska and Steffen 2013). A reduction in the ability to cope with changes in the environment consequently is a possible phenotypic change going along with the domestication process in a number of species (Hummer 1990; Price 1999; Oosthuizen et al. 2013).

Recent studies show that cognitive performance is reduced in some domesticated mammals (Dore et al. 1996; Fiset and Plourde 2013), although not in others (Albiach-Serrano et al. 2012). Probably depending on the given task, such differences could not be detected in all studies comparing wild and domestic lineages to one another (Range et al. 2012; Benhaim et al. 2013). Stuermer and Wetzel (2006) proposed that being well adapted to captive conditions, domesticated animals may perform better when facing a laboratory learning task irrespective of their cognitive abilities. In a similar fashion, wild animals may outperform their domestic congeners in other, non-laboratory learning tasks or both lineages may perform equally well.

To investigate the impact of domestication on learning and behavioural flexibility, we tested a wild type species, *Cavia aperea* (referred to as wild cavy) and the domesticated guinea pig *C. aperea* f. *porcellus* also known as *Cavia porcellus*. Both morphological and genetic data support a derivation of the guinea pig from *C. aperea* (Trillmich et al. 2004; Kruska and Steffen 2013), although there is also some evidence for a derivation from the closely related *Cavia tschudii* (Price 1984; Campler et al. 2009). Subsequently, we will refer to the two tested lineages as congeners following the most recent study of Kruska and Steffen (2013). Guinea pigs have been domesticated at least as early as 2500 BC (Sandweiss and Wing 1997). Due to this long-time scale and their short generation time relative to other, mostly larger, domesticated mammals, they are an excellent choice for investigating domestication effects. Both, wild cavies and guinea pigs, proved their ability to learn in cognitively challenging tasks before (Dringenberg et al. 2001; Lewejohann et al. 2010; Guenther et al. 2013). They, therefore, lend themselves as model species for further cognitive testing.

We used a number of behavioural tests and a cognitively challenging reversal learning task to investigate differences in behaviour and cognitive performance between the two lineages. In the cognition task, the animals first learnt to

associate a symbol and a reward and, once this association was drawn reliably, were rewarded for adjusting their learnt choice flexibly to one of the previously non-rewarded symbols that then served as the new rewarded cue.

In an earlier paper of our research group, a relationship between behavioural type, i.e. individual differences across three behavioural traits and performance in a task testing for associative learning and behavioural flexibility was found in wild cavies (Guenther et al. 2013). Here, we employ the same task to test whether guinea pigs and wild cavies differ in learning speed and flexibility. Additionally, we checked for the possibility that differences in cognitive performance between the two tested lineages were associated with differences in behaviour. Consequently, we measured each individual's aggressiveness (number of aggressive encounters in a social encounter test) and boldness (towards a novel object) and in addition sociopositive behaviour (number of sociopositive encounters in a social encounter test), which might possibly be the trait most affected by domestication in guinea pigs. If cognitive performance and the tested behavioural traits were linked, performance differences might be a by-product of a general shift in behaviour, caused by domestication processes. Looking at differences in morphology, we would suggest that the reduced brain case volume in guinea pigs might lead to a decrease in cognitive ability and consequently in performance in our learning task. A reduction in attention towards environmental changes would also favour this hypothesis with regard to the reversal learning step of our task testing for behavioural flexibility.

Presuming the persistence of linkages between behavioural and cognitive traits in the domestic guinea pigs, a number of other predictions can be hypothesized: boldness and aggressiveness were linked to performance in the associative learning task in wild cavies: bolder and at the same time more aggressive animals outperformed shyer and less aggressive ones. As guinea pigs should have become less attentive towards changes in their environment and less cautious towards predation threats over the course of domestication, it is hard to predict how they would react to a novel object introduced in their home enclosure. Being less attentive, they might just not inspect the novel object as closely as the wild cavies would, but at the same time being less cautious towards a, possibly threatening, object, they might also be faster to touch the object out of mere curiosity. However, with regard to aggressiveness being positively linked to learning performance in the wild lineage, we would predict the less aggressive domestic lineage to perform slower in the associative learning task than their wild congeners. In the reversal learning, in which more aggressive wild cavies needed more trials to reverse the learnt association, while boldness did not influence acquisition speed, guinea pigs should be able to outperform

their wild congeners. In accordance with a reduction of aggressiveness, we expect guinea pigs to show more sociopositive behaviour although we do not have prior expectations on how this shift in expression of social behaviour might be linked to cognitive performance.

Materials and methods

Animals and housing

Guinea pigs

Multicoloured and short-haired Guinea pigs are kept at Bielefeld University for more than 30 years and regularly interbreed with animals obtained from different local breeders to prevent inbreeding. The 21 guinea pigs that served as test subjects were housed in indoor enclosures in same sex groups consisting of 4–5 animals each. Enclosures measured approximately 2.5 × 1 m and were bedded with a 5-cm-thick layer of wood chips. Guinea pig chow, hay and water were available ad libitum and were supplemented with fresh greens several times a week and a weekly addition of 1 g/l vitamin C in the water. We tested 8 male and 13 female guinea pigs housed in five groups in our learning task. While eight males and four females started the test at an age of 21–30 days, the remaining nine females were about a quarter of a year old at the onset of testing. Guinea pigs mature at an age of approximately 30 days (Sachser et al. 1998) and consequently all animals tested were mature or reached maturity during testing.

Wild cavies

Our research group recently showed that the performance of wild cavies in the reversal learning task is linked to their behavioural type (Guenther et al. 2013) and we re-analyse these data here for a direct comparison with guinea pigs. Wild cavies are kept at Bielefeld University for more than 30 years and are outbred with wild-caught individuals regularly to prevent the population from potential domestication effects. Tested cavies were kept in outdoor enclosures (15 m²) with pens for shelter in groups of 5–6 males or, in case of the females, together with their mothers in groups of comparable size during testing. Pens were bedded with a 5-cm-thick layer of wood chips, while the enclosures had partly sandy ground and stone surface. Guinea pig chow, hay and water were available ad libitum and were supplemented with fresh greens several times a week and a weekly addition of 1 g/l vitamin C in the water. Twenty-one cavies, 13 males and 8 females entered the test at an age of 21–22 days. All animals were kept under natural photoperiodic conditions.

Ethical note

All experimental procedures comply with German animal protection laws. Animal facilities were approved (dated 18 April, 2002) for keeping and breeding wild cavies and guinea pigs for research purposes by the local government authority responsible for health, veterinary surveillance and food monitoring.

Behavioural traits

For all tests, the focal animal was separated from its group mates in a compartment of approximately one-third of the home enclosure. Pilot studies revealed that individuals were not participating in the learning task when visually isolated from their group mates, possibly due to a higher stress level. Therefore, we used a wire-mesh divider in the learning task that allowed visual contact to the group members. For the behavioural tests, the divider was opaque.

Novel object task

All guinea pigs were mature at the time they were tested in the novel object task. Each animal was separated from its group mates and gently chased under a shelter before a yellow rubber duck of 10 cm height was placed in the middle of the testing compartment as the novel object. The behaviour of the focus animal was video taped for 15 min. The latency until the duck was touched was taken from the videotapes, measuring from the moment the guinea pig was allowed to view and enter the test compartment again. If the animal did not touch the object within 15 min, the test was stopped and the animal scored a maximum latency of 900 s.

Social encounter test

Aggressiveness and sociopositive behaviours of the guinea pigs were measured in a social encounter with a random and unfamiliar male stimulus guinea pig. As in the novel object task, the younger animals were tested after and the older animals prior to the learning task. All animals were mature at the time of testing. The stimulus animal was put in the testing compartment 10 min prior to the test to allow familiarization with the surroundings. Subsequently, the focal animal was transferred to the testing compartment and confronted with the stimulus male for 15 min. Aggressive behaviour, i.e. fixation, demonstrating a curved body posture, chasing, teeth chattering, attacking and snapping as well as sociopositive behaviours, i.e. nudging, naso-nasal and naso-anal sniffing were counted and noted down by an experienced experimenter who was present throughout the confrontation to be able to intervene immediately if a fight escalated. However, no confrontation

had to be interrupted. We additionally analysed the sociopositive behaviours from the social encounter test in wild cavies as these data had been taken, but not considered in the previous analysis published in (Guenther et al. 2013) to achieve a better comparability between species.

Associative and reversal learning

Ten guinea pigs entered the learning test immature and prior to the behavioural tests, while the mature animals had been tested in the behavioural tests before participating in the learning test. Testing of wild cavies and guinea pigs was done similarly with one exception: The wild cavies were tested in a 1 m² arena placed in their home enclosure build of white plastic, 50 cm high and open on top and one side (see Fig. 1a). The open parts were covered with wire mesh. Guinea pigs were tested in an equally sized separable part of their home cage with the focal individual separated from its group by a wire-mesh divider (Fig. 1b). To avoid social learning effects, the task was set up orthogonal to the divider so that individuals outside the learning compartment could not recognize the different symbols used in the task. The experiment was set up on a 31 × 11 cm white plastic board placed on the bedding. The learning test started after a training phase in which the guinea pigs were trained to knock over a cylinder to reach a piece of cucumber hidden beneath it. Before each training trial started, the guinea pig was gently chased under a shelter placed on the opposite side of the enclosure than the testing board. The entrance as well as the view on the experimental setup was blocked by a second shelter put upright. A hollow plastic cylinder of grey colour (10 cm in height and 3.7 cm in diameter) was put up in the centre of the board for 15 min. The cylinder was closed on top with a rubber plug and open on the bottom. Two drill holes 0.2 cm in diameter allowed subjects to smell the cucumber when the cylinder was set up. The shelter blocking the access to the task was removed and the animal thus allowed to approach the setup. First, the cylinder covered the cucumber half. As soon as an individual consumed the piece of cucumber in three consecutive trials, the cylinder covered the reward completely and had to be knocked over three times in order to obtain the reward and pass on to the test. Each animal received between one and two training sessions a day consisting of four consecutive trials each with a minimum pause of 2 h in between. If an animal did not solve the training within 20 trials, it was excluded from further testing which was the case for three guinea pigs and three wild cavies (Table 1).

In the learning trials, three identical cylinders were put up on the board in 10 cm distance to one another. Each of them was baited with a piece of cucumber. While two cylinders were closed with a rubber plug on both sides, one

Fig. 1 Testing arena used for wild cavies (a) and testing compartment used for guinea pigs (b). Both shown from above, and experimental setup (similar in both tested lineages) shown from the front (c). In (a) and (b) xxx indicates wire mesh, light grey the sand that covers the ground of the testing arena in case of the wild cavies and wood chip layer in case of the guinea pigs. Testing took place on a 10 × 50 cm² white plastic board in the centre of the testing arena/compartment in both species

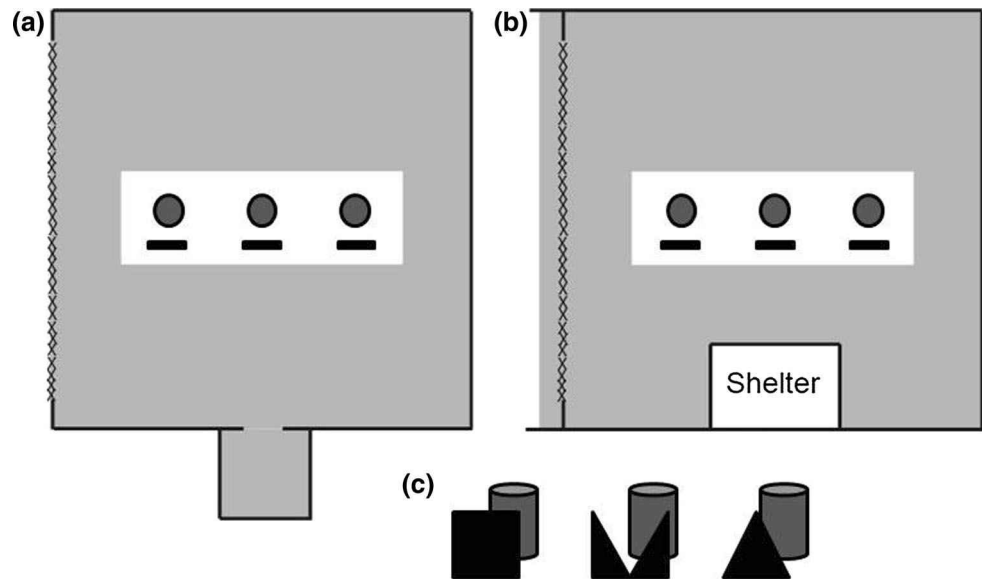


Table 1 Participants in the personality and cognition tasks and solvers of the different steps of the cognition task (absolute numbers/%)

	Personality participated (%)	Training participated (%)	Solved (%)	Initial learning (%)	Solved (%)	Reversal learning participated (%)	Solved (%)
Guinea pigs	24/100	24/100	21/88	21/88	19/79	17/70 ^a	10/41
Cavies	21/100	21/100	18/86	18/86	11/52	9/43 ^a	6/29

^a Two individuals that solved the initial learning were not available for testing in the reversal learning and thus were excluded from further analysis

remained open on the bottom and thus the cucumber could be reached by knocking this cylinder over. A triangle, a square and an M-shaped symbol were used as learning cues, assigned randomly to the individuals. All symbols were 10 cm in height and made of black plastic. The symbols were leaned against the testing board each in front of a cylinder from the guinea pigs' point of view. In the initial learning, always the same symbol leaned in front of the rewarded cylinder. The symbols were arranged randomly in their sequence with the restriction that one position was rewarded in no more than three consecutive trials. The cylinder touched first in a trial with the nose counted as the subject's choice. As in the training, each animal received between one and two test sessions per day with a minimum pause of 2 h in between. We considered the association between the symbol and the reward to be drawn if an animal chose correctly in at least eight out of ten consecutive active trials. If the animal did not choose a symbol within 15 min, the trial was scored as passive.

Once the initial learning was accomplished, the rewarded symbol changed and the reversal learning started. Choosing correct in eight out of ten consecutive active trials this time was considered a successful reversal of the learnt association. Animals dropped out of the test if they were not active, i.e. did not choose a symbol in twenty

consecutive trials or did not learn the association in fifty active trials. The number of active trials needed to solve the associative as well as the reversal learning was taken as a measurement of learning speed. Animals that already failed to solve the training were not considered in the two learning tasks, while those that participated actively but did not meet the criterion in the maximum number of trials in either the initial or reversal learning scored 50 trials.

Data analysis

Linear mixed effect models (LMM) were used to analyse sex and age differences in behavioural traits and cognitive performance in the guinea pigs as well as sex effects in the cavies. Consequently, we used sex and age at the onset of testing as fixed effects and relatedness between individuals as a random effect in the guinea pig models, while only sex served as a fixed factor in the cavy models where all tested individuals were of similar age at the onset of testing. However, no significant difference between the two age classes was found in guinea pigs and thus we used both age classes when testing for differences between lineages. LMM models were run to test for differences in behavioural traits and cognitive performance between guinea pigs and cavies by including sex and species as fixed

Table 2 Correlations between behavioural traits and cognitive performance in guinea pigs and cavies

Correlation	Species	<i>R</i>	CI _{min}	CI _{max}	<i>p</i> value
Boldness–aggressiveness	Cavies	0.62	0.26	0.83	0.003
Boldness–sociopositive behaviour	Cavies	0.81	0.59	0.92	<0.001*
Boldness–association learning	Cavies	0.79	0.48	0.92	0.002
Aggressiveness–association learning	Cavies	0.38	0.06	0.7	0.046
Sociopositive behaviour–association learning	Cavies	0.89	0.70	0.96	<0.001*
Aggressiveness–reversal learning	Cavies	0.87	0.97	0.5	0.02
Boldness–aggressiveness	Guinea pigs	0.77	0.52	0.9	<0.001
Sociopositive behaviour–association learning	Guinea pigs	−0.62	−0.83	−0.26	<0.001
Sociopositive behaviour–reversal learning	Guinea pigs	−0.99	−0.99	−0.95	<0.001

The correlation coefficients for boldness and aggressiveness were multiplied with -1 in order to achieve more intuitive values with positive indices indicating bolder and at the same time more aggressive animals. All *p* values with the exception of the values labelled with * are corrected for multiple testing but see the “Materials and methods” section for details

effects and relatedness between individuals as a random effect. However, not all of these models followed the assumption of normally distributed residuals smoothly, and thus, we decided to additionally run a nonparametric analysis, i.e. permutation based analysis of variance (PERMANOVA) for each of these comparisons. The results of these analyses did not differ qualitatively from the previous LMM approach. Thus, and to keep the results comparable to the previous ones on wild cavies (Guenther et al. 2013), we decided to report the approved LMM-based results throughout the paper.

To find the model fitting our data best, we compared Akaike information criterion values (AIC’s). Individual phenotypic values (best linear predictors, short BLUPs) taken from the LMM models were used to correlate behaviours and cognitive performances. We corrected for multiple testing in cases where multiple correlations were used to test for a single hypothesis using false discovery rate adjustment following (Garcia 2004), as it has been done with the dataset on wild cavies (Guenther et al. 2013). However, we refrained from correcting the additionally ran analyses on sociopositive behaviour in wild cavies for multiple testing. As both correlations with sociopositive behaviour are strong (*p* values range below 0.001), we are nonetheless confident to report reliable effects.

Data were analysed with the statistical software R (R Development Core Team 2012) and the corresponding R package nlme. PERMANOVAs were calculated using PRIMER 6.1.12 and the PERMANOVA+ 1.0.2 add-on (Clarke and Gorley 2006).

Results

Boldness, measured as the latency to touch the novel object, and aggressiveness, measured as the number of aggressive encounters in a social encounter, correlated positively in

guinea pigs as well as in cavies. An additional positive linkage between boldness and sociopositive behaviour was present in cavies, while absent in guinea pigs (see Table 2 for correlation estimates and significance levels and Fig. 2 for a graphical illustration). A comparison of behavioural traits between lineages reveals that guinea pigs were less aggressive (LMM, number of aggressive interactions, $N = 45$, $t = 2.56$, $p = 0.021$), and less bold (LMM, latency to touch the novel object, $N = 45$, $t = 2.17$, $p = 0.045$) than their wild congeners (see Fig. 3a, b), while none of the tested traits was expressed differently in the two age classes tested within the guinea pigs. With regard to sociopositive behaviour, we found an interaction effect of sex and species: guinea pig males showed sociopositive behaviour more frequently than females, while male cavies did not differ in the amount of sociopositive behaviour compared with their females (LMM, interaction between sex and species $N = 45$, $t = 2.57$, $p = 0.0164$, Fig. 3). While the sex difference in the number of sociopositive encounters was significant in guinea pigs (LMM, sex effect in sociopositive behaviour $N = 24$, $t = 2.82$, $p = 0.015$), no difference was apparent in cavies.

Comparing the cognitive performance between lineages, we found guinea pigs to learn the association within a mean number of 23.2 ± 3.7 trials, while cavies needed 38.0 ± 3 trials. This difference in associative learning speed between the two lineages was highly significant (LMM, species difference in associative learning speed, $N = 39$, $t = 2.56$, $p = 0.021$, Fig. 4). The difference in performance of guinea pigs and cavies did not persist into the adjacent reversal learning, but male individuals of both lineages needed less trials than females to rely on the newly rewarded cue successfully (LMM, sex difference in reversal learning speed, $N = 26$, $t = -2.19$, $p = 0.047$).

Concerning the linkage between cognitive performance and personality, some obvious differences were found between the two lineages. Sociopositive behaviour

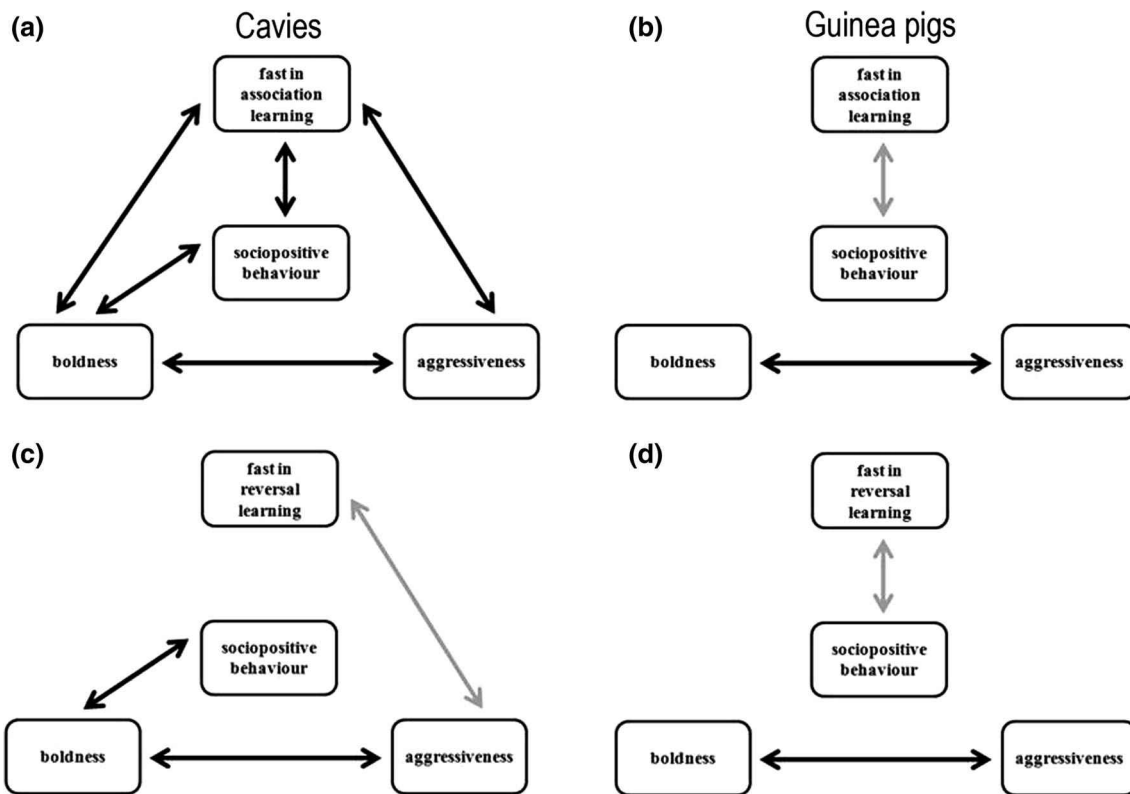


Fig. 2 Correlations between behavioural and cognitive performance in guinea pigs (a, c) and wild cavies (b, d) in the initial (a, b) and reversal learning step of the task (c, d). Positive correlations are

indicated by *black*, negative correlations by *grey arrows*. For the according statistics, see Table 1

correlated with learning in guinea pigs. In the associative as well as the reversal learning step of the task, those individuals that showed less sociopositive behaviour needed less trials to solve the task. Contrary to this finding, in the wild lineage, individuals that showed more sociopositive behaviour needed less trials to learn the association. However, this linkage did not persist in the reversal learning step in cavies. Additionally, positive correlations of associative learning and boldness as well as aggressiveness could only be found in the wild congeners. While the linkage between learning and aggressiveness inverted to a negative correlation in the reversal learning step, the one between boldness and learning disappeared (see Table 2 for statistics and Fig. 2 for a graphical overview).

Discussion

We found differences between domestic guinea pigs and wild cavies in behavioural traits as well as in cognitive performance. Guinea pigs were less aggressive and bold than their wild congeners. Additionally, guinea pig females showed less sociopositive behaviour than males, while there was no difference in cavies. The domestic lineage

learnt the association faster, while both performed equally in reversing this learnt association. The linkage between behavioural and cognitive traits was less pronounced in the domestic lineage and found only in a negative correlation between associative learning and sociopositive behaviour, while in cavies, aggression, boldness and sociopositive behaviour correlated with learning performance.

Our prediction regarding differences in aggressiveness between the two lineages was confirmed, as we found guinea pigs to be less aggressive than their wild congeners. Similar results have been found earlier in long-time behavioural observation as well as in spontaneous behavioural tests (Künzl and Sachser 1999; Künzl et al. 2003). While no overall difference in sociopositive behaviour was present, an interaction effect with sex occurred in the trait. Künzl and Sachser (1999) also found male guinea pigs to show more sociopositive behaviour than females, while no difference was apparent in wild cavies. Due to their reduced aggressiveness, which is most likely accompanied by a reduced probability of getting attacked or injured in social encounters, guinea pigs might initiate social contacts more frequently than wild cavies, where fights often lead to severe injuries (Sachser et al. 1998). Additionally, guinea pigs show much more courtship behaviour than their wild

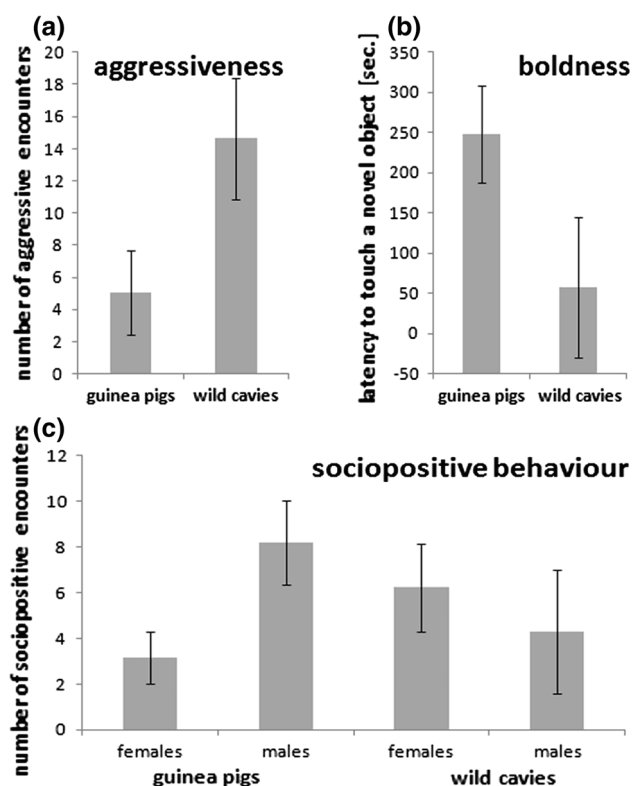


Fig. 3 Comparison of behavioural traits between guinea pigs and wild cavies for (a) aggressiveness. (b) Boldness and (c) sociopositive behaviour. Shown are the estimates of the LME models with standard errors

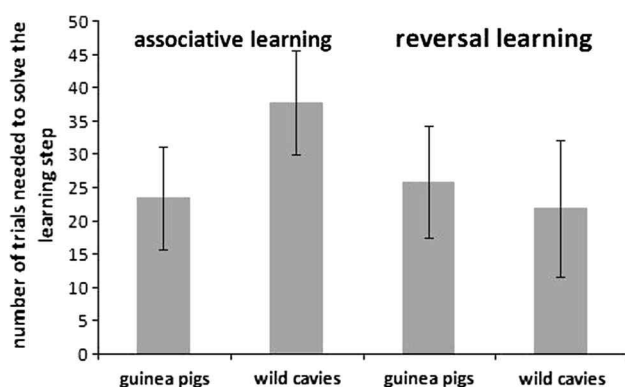


Fig. 4 Comparison of learning performance between guinea pigs and wild cavies in associative and reversal learning. Shown are the estimates of the LME model and their 95 % confidence intervals

congeners (Künzl and Sachser 1999), which might also be a reason why new individuals in social encounters are explored more intensely within the first few minutes, even if these are, like in our experiment, other males.

In the novel object task, guinea pigs scored higher latencies and can thus be considered to be less bold than their wild congeners. An equally strong positive relationship between boldness and aggressiveness was found in

guinea pigs and wild cavies. Although linkages between other behavioural traits were not apparent in guinea pigs that were found in cavies, the maintenance of the boldness–aggressiveness relationship points towards a strong evolutionary link in those two traits. Furthermore, the correlation might explain the higher latencies in the novel object task in guinea pigs that were selected over centuries for low aggression if being less aggressive goes along with being less bold. Additionally, a reduced attention towards their environment is normally one of the most noticeable characteristics of domestication (Price 1999).

The correlation between aggressiveness and boldness indicates the presence of a behavioural syndrome in the guinea pig, i.e. the correlation of behavioural traits. Additional recent evidence for behaviour shown in a social context to be repeatable over time exists in this lineage (Zipser et al. 2013). Taken together, these findings point in the direction of a personality structure in the domestic lineage, i.e. behavioural traits that correlate over context and are stable over time, as it has been confirmed in cavies before (Guenther et al. 2013). The positive linkage between aggressiveness and boldness found in both lineages is quite common across taxa in the animal kingdom (e.g. Wilson et al. 1994; Koolhaas et al. 1999), while the context of sociopositive behaviour is less well documented. In general, behaviour shown solitarily and in social contexts does not necessarily need to be related (Kilgour and Brigham 2013), and differences in the correlation of traits are common at least between species (Wilson et al. 1994). Interestingly, a positive linkage between boldness and sociopositive behaviour present in the wild cavies is absent in guinea pigs, leading to the conclusion that behavioural traits may also differ between lineages and can be modified by the domestication process. As guinea pigs have artificially been selected towards a less aggressive form, being less bold is a consequence when these traits correlate. Being less bold would also be linked to being less social. However, guinea pigs have at the same time been forced to live under higher densities than their wild relatives. Thus, showing more sociopositive behaviour would possibly be beneficial to them. Breaking up the correlation between boldness and sociopositive behaviour consequently seems to be one solution to adapt to the captive situation.

In the associative learning step of the cognition task, guinea pigs surprisingly outperformed wild cavies. A better performance of the domestic form in comparative cognitive tests is scarce across the literature (but see Millar 1975; Boice 1981) and often found only in single traits regarding the utilization of human social cues, while not in others (Hare et al. 2005; Bräuer et al. 2006; Hare et al. 2010). Still, our results resemble those of a spatial learning task comparing the learning speed of guinea pigs and wild cavies (Lewejohann et al. 2010), which suggests that the

faster learning performance is present on a broader scale and not only restricted to one task in guinea pigs. These findings cannot be explained by the brain size reduction of about thirteen percent in guinea pigs compared to wild caviés (Kruska 1988). A reduction in brain size in domestic species is often thought to influence cognitive performance negatively. Thus, at least in learning tasks, the wild congeners seem not to be able to take advantage of their larger brain structures. A reduced selection pressure on cognitive performance can also be ruled out as explanation for performance differences between lineages in this case. Still, guinea pigs might be simply better adapted to the testing procedure than their wild congeners. While the tested individuals of both lineages grew up under highly comparable conditions and consequently should all have similar ontogenetic experience with manmade enclosures and handling by human experimenters, over the course of evolution a genetically anchored adaptation to such situations and procedures may help the guinea pigs to perform better in our task. 89 % of the guinea pigs and 86 % of caviés solved the training step, possibly a hint that both lineages do not differ so much in how they deal with the setup. In particular, prenatal and early life experiences are known to play an important role in shaping the individual adult phenotype in behavioural (e.g. Del Giudice 2012; Perkeybile et al. 2013), as well as cognitive traits (Akman et al. 2004; Punzo 2004; Mehta and Schmauss 2011). As both lineages were kept under highly comparable conditions in our study and animals are used to the housing situation over decades, it is unlikely that such factors caused the learning difference.

A genetically anchored difference in the relationship between personality traits and learning performance thus seems to be the most likely explanation for our findings. The linkages found in wild caviés fit into the theoretical framework reviewed by Sih and Del Giudice (2012), as discussed in (Guenther et al. 2013). Although aggressiveness and boldness are still positively related in guinea pigs, both traits lack the direct linkage to associative learning. The predictions regarding the direction of behavioural linkages to cognitive traits have been made for animals exposed to natural selection. Being artificially selected by humans over centuries thus seems to have loosened the connection between behavioural traits and associative learning. Learning is essential to survive in the wild, e.g. when selecting food, identifying predators or recognizing members of a social group (Pearce 2008). Being of distinct personality types can favour different cognitive types when these influence the costs or benefits of dealing with a certain problem for a certain time (Sih and Del Giudice 2012). As an example for this coherency, fast-learning guppies (*Poecilia reticulata*) were at the same time bolder than their slow-learning conspecifics.

Boldness in this case was measured as how closely a predator was inspected and being bold was directly linked to a lower probability to survive (Dugatkin and Alfieri 2003). Bold guppies benefit from a fast learning performance as they will most likely inspect a task from close by and thus while exposed to predators. Shy fish, that will most likely inspect a learning task from a safe shelter for some time before approaching it, however, benefit from a slow learning speed if this reduces costs. A close linkage between behavioural and cognitive traits might thus help to optimize each individual's performance in relation to its facilities and needs. In captivity, a strongly reduced necessity to perform optimally might have resulted in a loosened linkage between cognitive and behavioural traits. An overall weaker connectivity of traits in guinea pigs might thus have resulted from the domestication process and the reduced necessity of an optimal performance under captive conditions. The most striking difference between lineages, however, is the linkage between sociopositive behaviour and association learning performance, which is positive in wild caviés, but negative in guinea pigs. The linkage in guinea pigs fits well to the theory that individuals that seek the presence of conspecifics also rely more on the group during foraging or when facing other physical problems and thus are probably better in social than in solitary learning (Sih and Del Giudice 2012) which has also received some empirical support (Katsnelson et al. 2011). Guinea pigs are normally co-housed with conspecifics in relatively small enclosures permanently and consequently can always rely on the presence of social partners. The natural situation, however, ranges from wild caviés living in large mixed sex groups under high-density conditions (Rood 1972) to animals that live in small one or two female and one male groups with solitary foraging occurring frequently (Asher et al. 2008). Consequently, it is not at all times helpful for the individuals of the wild lineage to rely on the presence of conspecifics, as it is likely that they face novel situations that require learning alone. A closer linkage between boldness, aggressiveness and learning in this case would instead combine individual coping strategies, which are independent from the social situation and individual learning abilities. As boldness is correlated positively with sociopositive behaviour in the wild lineage, this would also explain the positive correlation between sociopositive behaviour and learning.

In the reversal learning step of the task, the lineage differences in the links between behavioural traits and cognitive performance persist. Wild caviés show a negative relationship with aggressiveness, but no link to sociopositive behaviour. Guinea pigs show no link between aggressiveness and reversal learning speed, but a negative link with sociopositive behaviour. Unlike wild caviés,

guinea pigs seem not to face a trade-off between being fast in associative and reversal learning as it has been discussed before in the wild lineage (Guenther et al. 2013). As both lineages perform equally well in this task, it seems as if behavioural flexibility has not been altered over the course of domestication.

In summary, the domestication process altered behaviour as well as the personality structure in cavies. Important linkages between behavioural traits persist over the course of domestication while other, obstructive ones, are broken up. While the prediction of bolder and more aggressive individuals to have a faster cognitive style could be confirmed in wild cavies, they were not supported in guinea pigs. It thus seems as if the theoretical framework does apply to wild species, but not to animals that have been artificially selected over centuries.

Acknowledgments We wish to thank Mona Dersen, Janik Hundacker, Christian Meyer zur Heyde and Tobias Venema for their practical help during the experimentation phase. Lars Lewejohann and Oliver Krüger provided valuable comments on a former version of the Manuscript.

References

- Aboitiz F (1996) Does bigger mean better? Evolutionary determinants of brain size and structure. *Brain Behav Evol* 47(5):225–245. doi:10.1159/000113243
- Akman C, Zhao Q, Liu XZ, Holmes GL (2004) Effect of food deprivation during early development on cognition and neurogenesis in the rat. *Epilepsy Behav* 5(4):446–454. doi:10.1016/j.yebeh.2004.03.008
- Albiach-Serrano A, Brauer J, Cacchione T, Zickert N, Amici F (2012) The effect of domestication and ontogeny in swine cognition (*Sus scrofa scrofa* and *S. s. domestica*). *Appl Anim Behav Sci* 141(1–2):25–35. doi:10.1016/j.applanim.2012.07.005
- Asher M, Lippmann T, Epplen JT, Kraus C, Trillmich F, Sachser N (2008) Large males dominate: ecology, social organization, and mating system of wild cavies, the ancestors of the guinea pig. *Behav Ecol Sociobiol* 62(9):1509–1521. doi:10.1007/s00265-008-0580-x
- Benhaim D, Begout ML, Lucas G, Chatain B (2013) First insight into exploration and cognition in wild caught and domesticated sea bass (*Dicentrarchus labrax*) in a Maze. *PLoS One* 8(6):e65872. doi:10.1371/journal.pone.0065872
- Boice R (1981) Behavioral comparability of wild and domesticated rats. *Behav Genet* 11(5):545–553
- Brauer J, Kaminski J, Riedel J, Call J, Tomasello M (2006) Making inferences about the location of hidden food: social dog, causal ape. *J Comp Psychol* 120(1):38–47
- Campler M, Jongren M, Jensen P (2009) Fearfulness in red junglefowl and domesticated White Leghorn chickens. *Behav Proc* 81(1):39–43. doi:10.1016/j.beproc.2008.12.018
- Clarke KR, Gorley RN (2006) PRIMER v6: user manual/tutorial. PRIMER-E, Plymouth
- Clutton-Brock J (1989) A natural history of domesticated mammals. Cambridge Univ. Press, Cambridge
- Del Giudice M (2012) Fetal programming by maternal stress: insights from a conflict perspective. *Psychoneuroendocrinol* 37(10):1614–1629. doi:10.1016/j.psyneuen.2012.05.014
- Dore FY, Fiset S, Goulet S, Dumas MC, Gagnon S (1996) Search behavior in cats and dogs: interspecific differences in working memory and spatial cognition. *Anim Learn Behav* 24(2):142–149. doi:10.3758/bf03198962
- Dringenberg HC, Richardson DP, Brien JF, Reynolds JN (2001) Spatial learning in the guinea pig: cued versus non-cued learning, sex differences, and comparison with rats. *Behav Brain Res* 124(1):97–101. doi:10.1016/s0166-4328(01)00188-7
- Dugatkin LA, Alfieri MS (2003) Boldness, behavioral inhibition and learning. *Ethol Ecol Evol* 15(1):43–49
- Fiset S, Plourde V (2013) Object permanence in domestic dogs (*Canis lupus familiaris*) and gray wolves (*Canis lupus*). *J Comp Psychol* 127(2):115–127. doi:10.1037/a0030595
- Frank H (1980) Evolution of canine information processing under conditions of natural and artificial selection. *Zeitschrift für Tierpsychologie* 53(4):389–399. doi:10.1111/j.1439-0310.1980.tb01059.x
- Garcia LV (2004) Escaping the Bonferroni iron claw in ecological studies. *Oikos* 105(3):657–663. doi:10.1111/j.0030-1299.2004.13046.x
- Guenther A, Brust V, Dersen M, Trillmich F (2013) Learning and personality types are related in wild Cavies (*Cavia aperea*). *J Comp psychol*:in press. doi:10.1037/a0033678
- Hare B, Plyusina I, Ignacio N, Schepina O, Stepika A, Wrangham R, Trut L (2005) Social cognitive evolution in captive foxes is a correlated by-product of experimental domestication. *Curr Biol* 15(3):226–230
- Hare B, Rosati A, Kaminski J, Brauer J, Call J, Tomasello M (2010) The domestication hypothesis for dog's skills with human communication: a response to Udell and Wynne et al. (2008). *Anim Behav* 79(2):e1–e6. doi:10.1016/j.anbehav.2009.06.031
- Harker KT, Whishaw IQ (2002) Place and matching-to-place spatial learning affected by rat inbreeding (Dark-Agouti, Fischer 344) and albinism (Wistar, Sprague-Dawley) but not domestication (wild rat vs. Long-Evans, Fischer-Norway). *Behav Brain Res* 134(1–2):467–477
- Healy SD, Rowe C (2007) A critique of comparative studies of brain size. *Proc R Soc B Biol Sci* 274(1609):453–464. doi:10.1098/rspb.2006.3748
- Hediger H (1964) Wild animals in captivity. Dover Publications, Dover
- Hummer H (1990) Domestication, the decline of environmental appreciation. Cambridge University Press, Cambridge
- Huntingford FA (2004) Implications of domestication and rearing conditions for the behaviour of cultivated fishes. *J Fish Biol* 65:122–142. doi:10.1111/j.1095-8649.2004.00562.x
- Jensen P (2006) Domestication—from behaviour to genes and back again. *Appl Anim Behav Sci* 97(1):3–15. doi:10.1016/j.applanim.2005.11.015
- Katsnelson E, Motro U, Feldman MW, Lotem A (2011) Individual-learning ability predicts social-foraging strategy in house sparrows. *Proc R Soc B Biol Sci* 278(1705):582–589. doi:10.1098/rspb.2010.1151
- Kilgour RJ, Brigham RM (2013) The relationships between behavioural categories and social influences in the gregarious big brown bat (*Eptesicus fuscus*). *Ethology* 119(3):189–198. doi:10.1111/eth.12052
- Klefoth T, Skov C, Krause J, Arlinghaus R (2012) The role of ecological context and predation risk-stimuli in revealing the true picture about the genetic basis of boldness evolution in fish. *Behav Ecol Sociol* 66(4):547–559. doi:10.1007/s00265-011-1303-2
- Koolhaas JM, Korte SM, De Boer SF, Van Der Veeg BJ, Van Reenen CG, Hopster H, De Jong IC, Ruis MAW, Blokhuis HJ (1999) Coping styles in animals: current status in behavior and stress-physiology. *Neurosci Biobehav Rev* 23(7):925–935. doi:10.1016/s0149-7634(99)00026-3

- Koolhaas JM, de Boer SF, Buwalda B (2006) Stress and adaptation-toward ecologically relevant animal models. *Curr Dir Psychol Sci* 15(3):109–112. doi:[10.1111/j.0963-7214.2006.00417.x](https://doi.org/10.1111/j.0963-7214.2006.00417.x)
- Kruska D (1988) Effects of domestication on brain structure and behavior in mammals. *Hum Evol* 3(6):473–485. doi:[10.1007/bf02436333](https://doi.org/10.1007/bf02436333)
- Kruska DCT, Steffen K (2013) Comparative allometric investigations on the skulls of wild cavies (*Cavia aperea*) versus domesticated guinea pigs (*C. aperea f. porcellus*) with comments on the domestication of this species. *Mamm Biol* 78 (3):178–186. doi:[10.1016/j.mambio.2012.07.002](https://doi.org/10.1016/j.mambio.2012.07.002)
- Künzl C, Sachser N (1999) The behavioral endocrinology of domestication: a comparison between the domestic guinea pig (*Cavia aperea f. porcellus*) and its wild ancestor, the cavy (*Cavia aperea*). *Horm Behav* 35(1):28–37. doi:[10.1006/hbeh.1998.1493](https://doi.org/10.1006/hbeh.1998.1493)
- Künzl C, Kaiser S, Meier E, Sachser N (2003) Is a wild mammal kept and reared in captivity still a wild animal? *Horm Behav* 43(1):187–196. doi:[10.1016/s0018-506x\(02\)00017-x](https://doi.org/10.1016/s0018-506x(02)00017-x)
- Lewejohann L, Pickel T, Sachser N, Kaiser S (2010) Wild genius - domestic fool? Spatial learning abilities of wild and domestic guinea pigs. *Front Zool* 7:9. doi:[10.1186/1742-9994-7-9](https://doi.org/10.1186/1742-9994-7-9)
- Lindqvist C, Jensen P (2009) Domestication and stress effects on contrafreeloading and spatial learning performance in red jungle fowl (*Gallus gallus*) and White Leghorn layers. *Behav Proc* 81 (1):80–84. doi:[10.1016/j.beproc.2009.02.005](https://doi.org/10.1016/j.beproc.2009.02.005)
- Mehta M, Schmauss C (2011) Strain-specific cognitive deficits in adult mice exposed to early life stress. *Behav Neurosci* 125(1):29–36. doi:[10.1037/a0021952](https://doi.org/10.1037/a0021952)
- Millar RD (1975) Free-operant comparisons of wild and domestic Norway rats. *J Comp Physiol Psychol* 89(8):913–922
- Oosthuizen MK, Scheibler AG, Bennett NC, Amrein I (2013) Effects of laboratory housing on exploratory behaviour, novelty discrimination and spatial reference memory in a subterranean, solitary rodent, the cape mole-rat (*Georchus capensis*). *PLoS One* 8(9):e75863. doi:[10.1371/journal.pone.0075863](https://doi.org/10.1371/journal.pone.0075863)
- Pearce JM (2008) *Animal learning and Cognition: an introduction*. Psychology Press Ltd, East Sussex, New York
- Perkeybile AM, Griffin LL, Bales KL (2013) Natural variation in early parental care correlates with social behaviors in adolescent prairie voles (*Microtus ochrogaster*). *Front Behav Neurosci* 7. doi:[10.3389/fnbeh.2013.00021](https://doi.org/10.3389/fnbeh.2013.00021)
- Plyusnina IZ, Solov'eva MY, Oskina IN (2011) Effect of domestication on aggression in gray Norway rats. *Behav Genet* 41(4):583–592. doi:[10.1007/s10519-010-9429-y](https://doi.org/10.1007/s10519-010-9429-y)
- Price EO (1984) Behavioural aspects of animal domestication. *Q Rev Biol* 59(1):1–32. doi:[10.1086/413673](https://doi.org/10.1086/413673)
- Price EO (1999) Behavioral development in animals undergoing domestication. *Appl Anim Behav Sci* 65(3):245–271. doi:[10.1016/s0168-1591\(99\)00087-8](https://doi.org/10.1016/s0168-1591(99)00087-8)
- Price EO, Huck UW (1976) Open field behaviour of wild and domestic Norway rats. *Anim Learn Behav* 4(2):125–130. doi:[10.3758/bf03214022](https://doi.org/10.3758/bf03214022)
- Punzo F (2004) Early-life nutritional environment and spatial navigation in the water shrew, *Sorex palustris* (Insectivora). *J Environ Biol* 25(4):403–411
- Range F, Moslinger H, Viranyi Z (2012) Domestication has not affected the understanding of means-end connections in dogs. *Anim Cogn* 15(4):597–607. doi:[10.1007/s10071-012-0488-8](https://doi.org/10.1007/s10071-012-0488-8)
- R Development Core Team (2012) R. 2.13.2 edn. R developmental foundation for statistical computing, Vienna, Austria
- Réale D, Dingemanse NJ (2001) Animal personality. In: eLS. Wiley. doi:[10.1002/9780470015902.a0023570](https://doi.org/10.1002/9780470015902.a0023570)
- Rood JP (1972) Ecological and behavioural comparisons of three genera of Argentine cavies. *Anim Behav Monogr* 5:1–83
- Sachser N, Durschlag M, Hirzel D (1998) Social relationships and the management of stress. *Psychoneuroendocrino* 23(8):891–904. doi:[10.1016/s0306-4530\(98\)00059-6](https://doi.org/10.1016/s0306-4530(98)00059-6)
- Sandweiss DH, Wing ES (1997) Ritual rodents: the guinea pigs of Chinchua Peru. *J Field Archaeol* 24(1):47–58. doi:[10.2307/530560](https://doi.org/10.2307/530560)
- Sih A, Del Giudice M (2012) Linking behavioural syndromes and cognition: a behavioural ecology perspective. *Philos Trans R Soc Lond B Biol Sci* 367(1603):2762–2772. doi:[10.1098/rstb.2012.0216](https://doi.org/10.1098/rstb.2012.0216)
- Sih A, Bell A, Johnson JC (2004a) Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol Evol* 19(7):372–378. doi:[10.1016/j.tree.2004.04.009](https://doi.org/10.1016/j.tree.2004.04.009)
- Sih A, Bell AM, Johnson JC, Ziemba RE (2004b) Behavioral syndromes: an integrative overview. *Q R Biol* 79(3):241–277. doi:[10.1086/422893](https://doi.org/10.1086/422893)
- Stuermer IW, Wetzel W (2006) Early experience and domestication affect auditory discrimination learning, open field behaviour and brain size in wild *Mongolian gerbils* and domesticated laboratory gerbils (*Meriones unguiculatus* forma domestica). *Behav Brain Res* 173(1):11–21. doi:[10.1016/j.bbr.2006.05.025](https://doi.org/10.1016/j.bbr.2006.05.025)
- Trillmich F, Kraus C, Kunkele J, Asher M, Clara M, Dekomien G, Eppelen JT, Saralegui A, Sachser N (2004) Species-level differentiation of two cryptic species pairs of wild cavies, genera *Cavia* and *Galea*, with a discussion of the relationship between social systems and phylogeny in the Caviinae. *Can J Zool* 82(3):516–524. doi:[10.1139/z04-010](https://doi.org/10.1139/z04-010)
- West-Eberhard MJ (2003) *Developmental plasticity and evolution*. Oxford University Press, Oxford
- Wilson DS, Clark AB, Coleman K, Dearstyne T (1994) Shyness and boldness in humans and other animals. *Trends Ecol Evol* 9(11):442–446. doi:[10.1016/0169-5347\(94\)90134-1](https://doi.org/10.1016/0169-5347(94)90134-1)
- Zipser B, Kaiser S, Sachser N (2013) Dimensions of animal personalities in guinea pigs. *Ethology* 119(11):970–982. doi:[10.1111/eth.12140](https://doi.org/10.1111/eth.12140)