



Equine Research

Dumb or smart asses? Donkey's (*Equus asinus*) cognitive capabilities share the heritability and variation patterns of human's (*Homo sapiens*) cognitive capabilities



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ABSTRACT

Scientific evidence for intelligence in donkeys could expose their historical unmerited cognitive derogatory status. Psychometric testing enables quantifying animal cognitive capabilities and their genetic background. Owing to the impossibility to use the language-dependent scales that are widely used to measure intelligence in humans, we used a nonverbal operant-conditioning problem-solving test to compute a human-analogous IQ, scoring the information of thirteen cognitive processes from 300 genetically tested donkeys. Principal components and Bayesian analyses were used to compute the variation in cognitive capabilities explained by the cognitive processes tested and their genetic parameters, respectively. According to our results, IQ may explain over 62% of the cognitive variance, and 0.06 to 0.38 heritabilities suggest that we could ascribe a significant proportion to interacting genes describing the same patterns previously reported for humans and other animal species. Our results address the existence of a human-analogous heritable component and mechanisms underneath intelligence and cognition in probably one of the most traditionally misunderstood species from a cognitive perspective.

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Introduction

Donkeys' unmerited conception of problematic behavior curiously came into the scene at the same age in which the species was probably enjoying one of the most productive times for their functionality. During the Egyptian pharaonic times (Navas et al., 2016; Rossel et al., 2008), donkeys were not just herded for milk or meat production but were also usually ridden by the most notable personalities (Alkhateeb-Shehada, 2008; Bar-Oz et al.,

2013), which provided them with a distinguished role in society. Superstition-conjoined consequences together with their psychological misunderstanding relegated this animal to become one of the most cognitively detracted species of all times, as reported by the derogatory references found in several languages and cultures worldwide (Bough, 2010; Estaji and Nakhavali, 2011; Gregory, 2007; Way, 2014). This context has indirectly translated into donkeys facing one of their most worrying endangerment situations nowadays as a consequence of their lack of functionality (Navas et al., 2017b).

Assisted therapy has stepped into the functional scene of donkeys as it has been reported to facilitate effective recovery of spontaneous communication in people with affective and emotional disorders because of their empathic nature (Borioni et al., 2012), which may rely on the way they use their cognitive abilities to interact with humans (Sudekum Trotter and Baggerly, 2018). Increasing the scarce information relative to interindividual

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variability in cognition in equines (donkeys and horses) and their hybrids through research (Osthaus et al., 2013) may open a new path toward finding equine-specific genes (Momozawa et al., 2005b) involved in assisted therapy—desirable behavioral traits, increasing the profitability of selection strategies aimed at developing potential therapeutic lines, or providing knowledge that could be used to model or understand the underlying biological mechanisms behind cognitive processes in other species such as humans.

The historical interest in animal intelligence and cognitive learning processes was highlighted by the letters to the editor under the topic *Intelligence in animals* published by the Nature Journal from 1883 to 1904. This scientific context, based on the unavoidable relation established to related human characters, led to the definition of the general factor of intelligence or *g*. According to Deary et al. (2010), more than a century of empirical research provides conclusive evidence that a general factor of intelligence (*g*) exists, despite some claims to the contrary (Herrmann and Call, 2012). From their review, we could infer that *g* partially accounts for 40% to more than 50% of the differences in the performance between individuals on a given cognitive test (Locurto et al., 2013; Reader et al., 2011), and composite scores (intelligence quotient [IQ]) based on different tests are frequently regarded as estimates of individuals' standing on *g*. Other authors such as Kamphaus and Frick (2005) and Frick et al. (2010) suggest that the terms IQ, general intelligence, general cognitive ability, general mental ability, and intelligence are often used interchangeably to refer to this common core shared by cognitive tests.

Matzel and Sauce (2017) state that the rationale for most psychometric tests is roughly based on Spearman's (Spearman, 1904) observation that performance on a wide range of cognitive tasks is correlated and, as such, can be reduced to a single index of aggregate performance across a battery of diverse tests. That is, the more familiar term intelligence quotient (IQ) is used in humans as it summarizes the correlations observed between the scores of a particular individual on a wide range of cognitive abilities compared to the skills that such individuals must possess considering their chronological age (Reader et al., 2011). In the normal population, *g* (one of the existing psychometric constructs that summarize the correlations among different cognitive tasks in individuals) and IQ (what you score on a cognitive test from individuals) are roughly 90% correlated. Such a strong correlation enables using IQ as a standardized score of tests designed to measure *g*, with a high level of accuracy, and vice versa (OpenStax, 2014).

The influence of language on intelligence has been reported to be one of the most determining factors setting human and animal cognition apart (Dennett, 1994). There appears to be no evidence to date that nonhuman species understand recursion (Corballis, 2007). Because animals lack recursion (and human language is recursive), animals lack language (Premack, 2007). Traditional tests put a premium on language skills, making it necessary to develop and assess intelligence through nonverbal tests, for instance, those used in children with language difficulties or disabilities (DeThorne and Schaefer, 2004). In contrast to widely verbal or language-dependent scales used in humans, animals' cognitive ability assessment relies on interactive and observational tools focusing on the ability of the animals to interact with environment and everything on it through innovation, habit reversal or inhibition, social learning, or the responses to known and unknown stimuli.

Among other issues (Kaufman, 2018), two of the criticisms usually targeted at attempts to test for nonhuman *g* address the difficulty of developing standard tasks to be implemented across species and the presence of species specializations (Proops et al., 2009). Furthermore, leaving experimental conditions to assess species in their environment (Miklosi, 2015; Miklósi and Kubinyi,

2016) can be a challenging experience, especially when these species lack human-primate behavioral resemblance or mice in-depth knowledge of cognition genomics (Plomin, 1999).

Although these problems are lessened in studies in which comparisons are made among very similar species (Proops et al., 2009), literature rarely contrasts distant species. However, these difficulties could be overcome by implementing an extrapolation method. The quantification of cognitive capabilities in humans can be performed by considering tests of a very different nature but which assess the same underlying cognitive processes (Eysenck, 2018). Although tests measuring for the ability of individuals at specific cognitive processes may differ in what is measured and how, they commonly report a single psychometric construct per individual (Saklofske et al., 2017).

Only few examples of research involve cognitive processes from a genetic perspective, for instance, humans (Darst et al., 2015), mice (Galsworthy et al., 2005), or primates (Hopkins et al., 2014). Thus, research in the field still relies on phenotypical perspectives and rather suggests the genetic structure behind such processes than quantify it (Horowitz, 2014). In this context, human-nonhuman species extrapolations are rare (Anderson et al., 2017). *g* has proved to be responsible for 47% to 60% of the individual genetic variance in cognitive ability measures in nonhuman species such as primates (Locurto et al., 2013; Reader et al., 2011). This percentage of explained variability is similar to the fraction of variance explained by IQ reported for humans (40%–50%) (Kamphaus and Frick, 2005). Some studies have reported the existence of large interspecific (Osthaus et al., 2013) and intraspecific (Baragli et al., 2011) variation in cognitive processes in donkeys; no wide-scale populational study has been carried out, and despite being suggested (Proops et al., 2012), the genetic background behind them remains unexplored yet.

Therefore, the present research aims to develop a human-analogous animal IQ score and to study the populational variation and the inheritance patterns described in donkeys. The use of extensively genetically tested pedigree information can provide us with contrasting evidence to the popularly attributed dual misconception between intelligence and stupidity in donkeys. This approach seeks to respond to traditionally raised questions about the practical application of equine behavior and genetics affecting cognition and related factors (Hausberger, 2002) and also allows us to contrast the population distributions of donkey and human intelligence.

Materials and methods

Study sample and study background

The Andalusian donkey breed is currently recognized as an endangered autochthonous breed by the Spanish Official Catalogue of Livestock Breeds. Safeguard actions applied to this breed include the official recognition in the studbook of the breed and its breeding program, which took place on 26 December 2012. The whole pedigree file included 1017 Andalusian donkeys—272 jacks and 745 jennies—born between January 1980 and July 2015. The current Andalusian donkey population consists of 914 donkeys—246 jacks and 668 jennies—born from January 1980 to July 2015. The effective population size based on the individual inbreeding rate ($N_e F_i$) (\pm SD) was 17.81 ± 8.45 , whereas based on the individual coancestry rate ($N_e C_i$) (\pm SD), it was 41.88 ± 2.56 (Navas et al., 2017b). Direct records included the information of 300 Andalusian breed donkeys (78 jacks and 222 jennies). As the age range was not normally distributed ($P < 0.05$ Shapiro-Francia W' Test of normality), we used minimum, Q_1 , median, Q_3 , and maximum to describe the age range in our sample. The minimum

age was 0.27 months, Q_1 age was 29.76 months, median age was 77.04 months, Q_3 age was 129.07 months, and the maximum age was 270.40 months. Such wide age range was considered because the test battery used to assess cognitive processes was suitable for all animals included in the study and given the fact that we evaluate an endangered breed from which the information belonging to each individual is indispensable. The donkeys in the sample were the progeny of 93 jacks and 253 jennies. Parentage tests for each mating had been performed with 24 microsatellite molecular markers recommended by the International Society of Animal Genetics providing extensive indirect information on genetically tested pedigree from 724 ancestors.

Behavioral record registration

Before carrying out the behavioral assessment, we conducted a telephonic interview to survey the experience of the owners of the donkeys in the study to define the traits comprising the clusters to consider in the model. We interviewed owners about their donkeys' inherent cognitive abilities, the tasks that they should routinely accomplish on their farms, and the training/education methodology (or learning methods) owners regularly apply for their donkeys to learn such skills/tasks. Based on the answers the respondents gave, thirteen traits that were frequently alluded to during the interviews were chosen for evaluation (Supplementary Table S1). We discarded the rest of the features because of the anecdotal occurrence of their use or because they were redundant behavioral trait concepts that were merely labeled differently.

We organized the information derived from the interview for the thirteen behavioral traits in two clusters. The "cognition" cluster comprised seven traits that were directly related to nonspecific cognitive processes related to the ability of donkeys to perceive information from their environmental situation. The "intelligence" cluster comprised six traits related to cognitive processes or mental capacities of the donkeys to retain information from the

environment as knowledge to be applied toward adaptive responses within a specific context (Table 1). Table 1 defines each cognitive process or trait assessed and the human extrapolation. We translated these categorical traits into different linear scales, in which the donkeys scoring 1 meant they presented the lowest extreme behavioral pattern, and 5, the highest extreme one. We show the thirteen intelligence- and cognition-related traits considered and a detailed definition of the scores present in the scale in Supplementary Table S1.

We set the definition of the cognitive processes included in the study, defining the scales to measure them and establishing the possible nongenetic factors that may be exerting a modulating effect, by relying on the protocols in Momozawa et al. (2005a) and establishing their analogies with human cognitive processes (Navas et al., 2017a) (Figure 1, Table 1, and Supplementary Table S1). The thirteen cognitive processes were divided into seven direct on-field general cognitive process-related traits and six specifically related to intelligence cognitive process traits, according to principal component analysis (PCA) criteria, as described in Navas et al. (2017a). The standardization and development of the tests and scales was described in a previous stage of the study (Navas et al., 2017a; Navas González et al., 2018b) and is summarized in Figure 1. Statistical verification that tests being used are in fact measuring the constructs they are intended to measure and whether they can do so with internal reliability was performed in two previous studies (Navas et al., 2017a; Navas González et al., 2018a).

We registered all records describing the cognitive ability of the donkeys during the development of a six-stage operant conditioning test (Figure 1). The same trained appraiser registered all the information concerning the four behavioral variables for all the stages and animals. The donkeys were each given a maximum of 450 seconds to complete the operant conditioning test (75 seconds per phase and treatment implemented). No additional time was provided for the donkeys to complete the test.

Table 1
Definition of the thirteen cognitive processes comprising the intelligence and general cognition clusters studied in donkeys and their human analogy

Cluster	Cognitive process	Definition	Human analogy
Intelligence	Concentration	The animal collaborates during the assessment session and does not get distracted by the environment.	Attention (Moran, 2011) ^a
	Curiosity	The animal is interested in the novel stimuli being presented and moves toward them.	Curiosity (Kidd and Hayden, 2015) ^a
	Memory	The animal remembers the stimuli being presented.	Memory (Goshen and Yirmiya, 2007) ^a
	Stubbornness	The donkey rejects following the requests of the assessor.	Cognitive rigidity (Buzzichelli et al., 2018)/ decision-making (Secchi and Bardone, 2009) ^b
	Docility Alertness	The donkey easily follows the orders of the instructor. The animal shows a vigilant or alert status focusing on the stimulus around.	Docility/decision-making (Secchi and Bardone, 2009) ^b Alertness (Oken et al., 2006) ^a
General cognition	Dependence	The donkey is comfortable when separated from the main herd	Separation anxiety (Littenberg et al., 1971) ^b
	Trainability	Ability of the animal to be trained into the fulfillment of the tests	Cognitive training (Sternberg, 1981) ^b
	Cooperation	The donkey cooperates with its handlers during the daily tasks	Cognitive cooperation (Wilson et al., 2004) ^a
	Emotional stability	The animal is not predictable from one to another stimulus	Anticipation (Roca et al., 2011; Murphy et al., 2015)/ predictability (Namikawa et al., 2013) ^b
	Perseverance	The animal is patient when completing several sequential tests.	Patience (Wang and Ruhe, 2007). Related to decision-making. Patience is studied as a decision-making problem, involving the choice of either a small reward in the short term, against a more valuable reward in the long term (Coutlee and Huettel, 2012) ^b
	Get in/out of stables	The animal shows no problem when leaving or entering its housing facilities.	Fear (Hofmann, 2008)/cognitive appraisal (Folkman et al., 1986)/ coping (Lazarus and Folkman, 1984) ^b
	Ease of handling	The animal shows sympathy toward humans.	Cognitive empathy (Smith, 2006)/attitudes toward animals (Taylor and Signal, 2005; Sharp et al., 2006) ^b

Definitions and clustering criteria accessed from Navas et al. (2017a,b) and Sparrow and Davis (2000).

^a Addressed as cognitive processes in literature themselves.

^b Addressed to involve several underlying cognitive processes in literature.

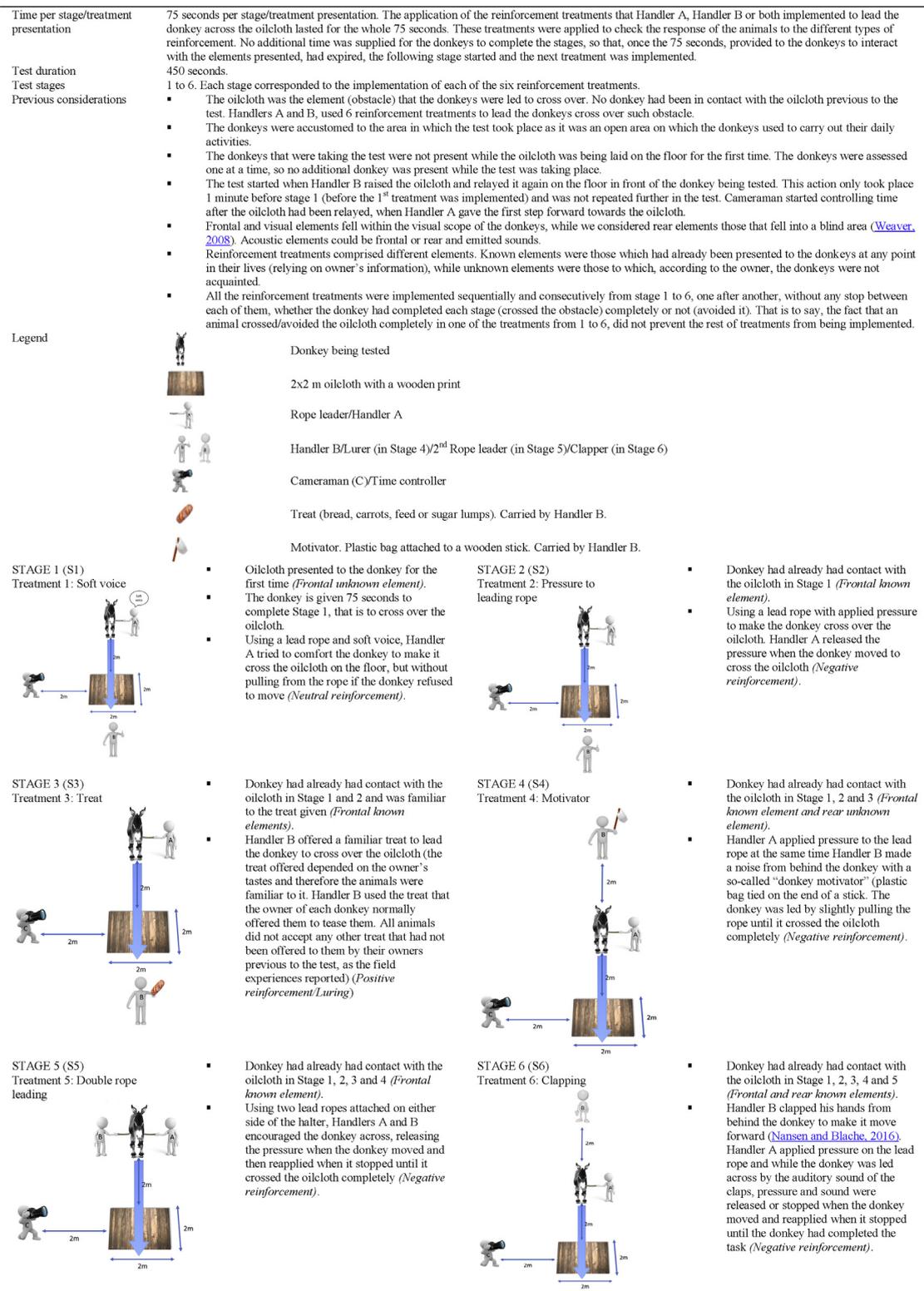


Figure 1. Operant-conditioning behavioral test to assess for the thirteen cognitive processes in the study. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Operant conditioning behavioral test

The operant conditioning behavioral test was carried out in an open area to which the donkeys were previously accustomed to (it was part of the area over which the donkeys performed their daily

activities). We exposed each animal to six reinforcement treatments consecutively, one at each of the six stages within the operant conditioning test. At each phase, handler A and handler B used each of the six different reinforcement treatments to lead the donkeys to cross over an oilcloth lying on the floor. These

treatments could comprise unknown elements (the animal was not familiar to them) or known factors (to which the animal was already familiar). These elements could be visual (elements fell within the visual areas of the donkeys) and/or acoustic (elements generated sounds, i.e., “motivator” or claps, although they may or may not fall within visual areas) and were presented to the donkeys from different positions (from the front or from a rear position always at 2 meters away from the animals). A cameraman (handler C) simultaneously videotaped the experiences (1080 p, 50 Hz, shutter speed: 1/250 seconds) to assess the donkey’s performance after the field experiences and to test for intraobserver discrepancies. The cameraman (handler C) controlled timing. We show a detailed description of the operant conditioning test in [Figure 1](#) and [Navas González et al. \(2018b\)](#).

Test and scoring system reliability

We did not note intraobserver discrepancies as all the scores obtained on the field matched those obtained after reviewing the tapes again. We run a Cohen’s κ test at a preliminary stage of the study to test for interobserver reliability and determine if the three appraisers’ judgment agreed on the scores of 50 individuals (16.67% of the total sample) for the score at the thirteen cognitive processes assessed. Cohen’s κ determined whether the repeatability of the model was enough to delete the effect of the appraiser from the model, providing a measure of the accuracy of scoring of the appraisers. Then, 95% confidence intervals (95% kappa CI) were computed according to 95% kappa IC = $\kappa \pm 1.96 \text{SE}\kappa$, where $\text{SE}\kappa = [\text{po}(1-\text{po})/n(1-\text{pe})^2]^{0.5}$ with the Crosstabs procedure of SPSS Statistics for Windows, version 24.0, IBM Corp. (2016). This preliminary analysis aimed at testing for the reliability of the scoring system, which proved to be highly reliable as there was highly statistically significant perfect agreement between the three appraisers’ judgments when scoring for the thirteen cognitive processes tested during the development of the operant conditioning test. There was highly statistically significant and from substantial to almost perfect agreement among the three observers of the preliminary test for repeatability for all the traits. We present the results for this preliminary study in [Supplementary Table S2](#).

Donkey’s intelligence quotient (IQ)

In human terms, mental age scores how an individual performs intellectually for a particular cognitive process, compared to the average performance that should be expected for that individual for that same cognitive process at its current chronological age ([Gerrig and Zimbardo, 2002](#)).

Current human IQ tests set the median raw score of the norming sample as IQ 100, i.e., when chronological and mental ages are equal or when a particular individual can reach the score that would be expected to reach considering its chronological age ([Hunt, 2010](#)). Then, each standard deviation (SD) unit from this value is scored up or down at increasing or decreasing intervals of 15 IQ points ([Gottfredson, 2009](#)). We computed the mean score obtained by the donkeys in the population under study at the multiphased operant conditioning test ([Supplementary Videos 1–6](#)) for each of the thirteen cognitive processes (scored 1 to 5) to develop an analogous animal scale. Then, using the variation reported for humans as a reference ([Hunt 2010](#)), we focused on the highest mean score in the scale (from 1 to 5) that was reached on average by any donkey of the lowest age level possible for each cognitive process ([Figures 2 and 3](#)). Then, we set such score as the average range (IQ 100), addressing the mental age at which a donkey, in particular, would be expected to reach that score for that specific cognitive process. This score set the starting point from which to

move up or down in the scale from 1 to 5 ([Table 2](#) and [Supplementary Table S1](#)) to set the IQ categories above the average (above average and very superior) ([Figure 3](#)). Quantitatively, we made these increases/decreases following 15-point intervals per SD unit.

To extrapolate the results to humans, when this mental age matched the chronological age of a particular donkey, we considered its IQ to be within the average range and thus analogous to human IQ 100. We classified the donkeys below this score at which the mental age was equal to the chronological age to be below the average IQ range ([Figure 3](#)). Overestimation of individuals very below or above the average is likely to occur because of the donkeys being able to succeed in reaching the highest average level (5) for the different processes at very early ages.

The mental age of each donkey, hence IQ, was computed as the average of the mental ages or IQs reported for all of the thirteen cognitive skills for each animal. We calculated IQ through the following mathematical equation: $\text{IQ} = (\text{mental age}/\text{chronological age}) \times 100$ (NCME, 2017).

Variance in problem-solving multistage cognitive test

A PCA was carried out to compute the variation in IQ explained by the cognitive processes tested.

Humans’ and donkey’s IQ distribution comparison

We compared humans’ and donkeys’ IQ distributions through the calculation of polynomial regression equations (2nd order) and R squared (R^2) values as shown in [Figure 2](#) and compared through an analogous scale in [Figure 3](#). To score the difference between distributions, we calculated the percent of explained SD or the percent by which the SD of the errors is less than the SD of the dependent variable, following the equation suggested by [Nau \(2014\)](#):

Percent of explained SD = $(1 - \sqrt{1 - R^2}) * 100$, with R^2 being R squared.

Genetic analysis, predicted breeding values, and descriptive statistics (PBV Bayesian accuracies)

Our study aimed at obtaining estimators for fixed effects and covariates, variance components, heritabilities, and breeding values for cognitive process–related traits in Andalusian donkeys, through single record mixed animal model procedures, as all the characters were scored only once in the lifetime of the individual through Bayesian multivariate analyses using the Multiple Trait Gibbs Sampling for Animal Models package (MTGSAM) ([Van Tassel and Van Vleck, 1995](#)). We obtained a single chain of 550,000 cycles, discarding 50,000 (burn-in), and using thinning intervals of 200 cycles to retain sampled values, which reduced the lag correlation among thinned samples. The convergence criteria used implied the change in the log-likelihood of the function in successive iterations and were less than 10^{-10} . Gibbs sampling procedures enable building and saving a random number or the total number of samples of variances obtained in the iterative process (2058 solutions in our case). Then, for each sample of variances saved, the genetic parameters could be calculated and assessed to obtain descriptive statistics such as mean, SD, variance, and standard errors, which could provide us with a perspective of the existing variability. Univariate analyses were carried out to compute the heritability of each trait to avoid the distortion that could be caused by the effects of epistasis among features (calculated then within residual variance). Then, bivariate analyses were used to calculate the correlations between each possible combination of the thirteen

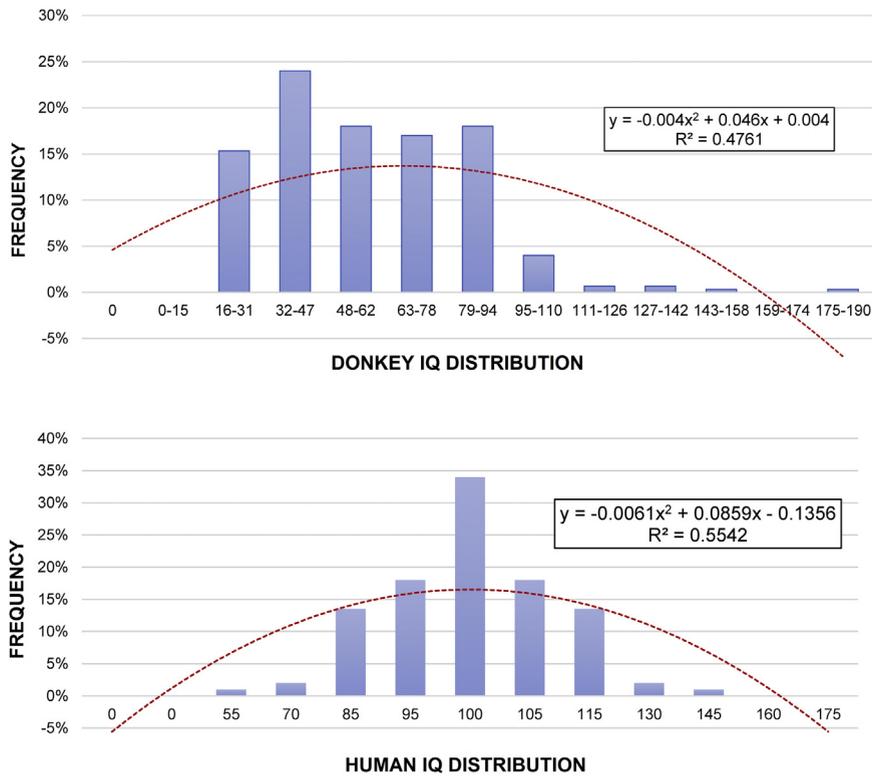


Figure 2. Donkey sample and human population IQ distribution graphic, R squared, and polynomial regression equation (second order). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

characters assessed to quantify such possible epistatic effects through genetic correlations. From a genetic perspective, the genetic correlation between two traits is the correlation between the genetic influences on a trait and the genetic influences on a

different trait estimating the degree of pleiotropy or causal overlap between both traits, whereas phenotypic correlation is a measure of the strength (consistency, reliability) of the relationship between performance in one trait and performance in another trait. On the

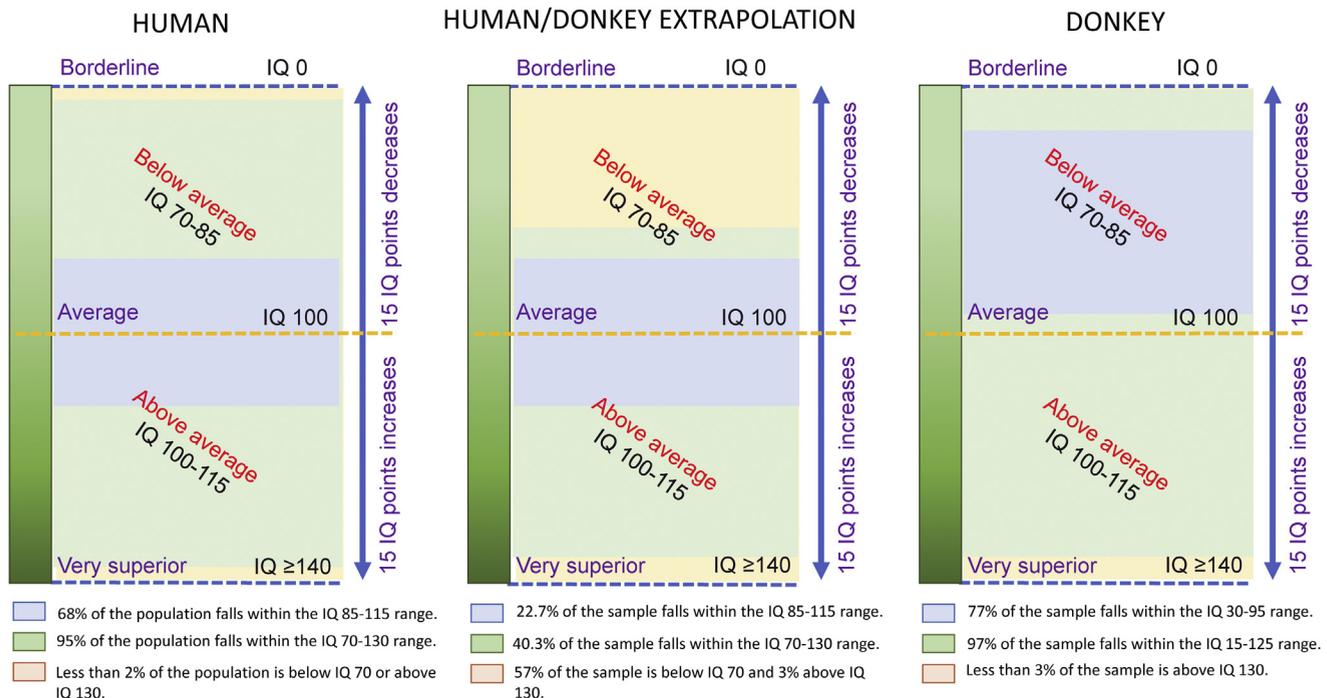


Figure 3. Distribution of humans' and donkeys' IQ and human-donkey IQ extrapolation, frequency representation, and scale description. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 2
Mental age ranges (in months) in Andalusian donkeys for the thirteen cognitive processes studied

Cluster	Items/scores	1	2	3	4	5
Intelligence	Concentration	Below average	Below average	Average	3	17
	Curiosity	Below average	Below average	Below average	Average	21
	Memory	Below average	Below average	Average	3	17
	Stubbornness	Below average	Below average	Below average	Average	27
	Docility	Below average	Below average	Below average	Average	27
	Alertness	Below average	Below average	Below average	Average	3
General cognition	Dependence	Below average	Below average	Average	3	21
	Trainability	Below average	Below average	Average	3	38
	Cooperation	Below average	Below average	Below average	Average	17
	Emotional stability	Below average	Below average	Below average	Average	27
	Perseverance	Below average	Below average	Below average	Average	3
	Get In/Out of Stables	Below average	Below average	Below average	Below average	Average
	Ease at Handling	Below average	Below average	Average	3	17

The average level was set at the mean score reached for each cognitive process at the age range of ≤ 1 month.

contrary, environmental correlations describe the relationships between the environments affecting two traits. The relationship between phenotypic correlations and their components is defined through $rP = rG + rE$.

Then, we estimated predicted breeding values (PBVs) and systematic deviation for all animals in the relationship matrix. We calculated Bayesian PBVs directly with the MTGSAM software (Supplementary Table S3). To assess the accuracy of PBVs, we calculated the posterior distribution of each parameter sampling uncorrelated realizations from the Gibbs chain with the PULLDAT application of the MTGSAM software. We thinned the chain of samples until the correlation of adjacent samplings was approximately 0 to assess the distribution, calculate mean, SD, variance, and standard error of breeding values (Supplementary Table S4).

The multitrait animal model equation used for the analyses is as follows:

$$y = Xb + Za + \varepsilon,$$

where y is the vector of records for cognitive process–related traits, b is the vector of fixed effects to be estimated and X is the corresponding incidence matrix relating records to fixed effects, a is the vector of breeding values to be determined and Z is the corresponding incidence matrix, and ε is the vector of residuals. In this case, the fixed effects considered in vector b were assessment year (3 levels: 2013, 2014, 2015), sex (2 levels: male and female), and husbandry system (5 levels: intensive, semi-intensive, semi-extensive, contest, and extensive) plus the linear and quadratic effect of age at scoring as a covariable, as age could be expected to affect the ability of the individuals to solve out multistage problem-solving cognitive test to correct for its possible distortion. The variation coefficient for age in our sample is 0.73, which was based on the population's age distribution depicted in Navas et al. (2018). This population distribution may compromise the evaluation of our sample in more narrowly defined age ranges as they may not be representative of the whole population because of the unequal distribution of animals among the groups.

We chose the previously described combination of fixed effects as the bivariate correlations found between at least one of the fixed effects and each of the thirteen cognitive process–related traits were statistically significant ($P < 0.05$). A previous analysis was carried out to describe the effects and levels included in this model (Navas et al., 2017a).

The analyses included the relationship matrix of animals with direct records related through at least one known ancestor, considering the 1,017 animals in the historical pedigree. Considering the lack of previous experiences for cognitive and intelligence traits in donkeys, we used the phenotypical variance of each character and the existing phenotypical correlations between each

possible pair combination for the estimation of the starting point to seek for the convergence of additive genetic variance component (multiplying them by 0.2). Then, we did the same for residual variances (multiplying them by 0.8) and genetic and phenotypic correlations to obtain specific variance components and estimates of fixed and random effects for each trait in multivariate analyses. The standard errors of genetic correlations were derived directly from the MTGSAM analyses. After the analyses reached convergence and we obtained genetic parameters, we estimated PBVs for all animals in the relationship matrix and we obtained fixed effect estimates.

Results

Donkey's intelligence quotient (IQ)

Table 2 and Supplementary Table S5 show the mental age ranges and descriptive statistics for each of the thirteen cognitive processes studied. Human (University of Minnesota, 2015) and donkey IQ distributions, polynomial regression equations (2nd order), and R squared (R^2) values are shown in Figure 2 and compared through an analogous scale in Figure 3. The percent of explained SD for donkeys' IQ was of 27.62%, whereas for humans, it was 33.23%.

Variance in problem-solving multistage cognitive test

The PCA revealed two components whose eigen values were higher than 1 (Table 3), which together explained 72.14% of the cognitive variation between donkeys. However, the eigen value of the second component (PC2) was only slightly higher than 1. The

Table 3
Results of the principal components analysis for the 300 Andalusian donkeys

Cluster	Cognitive process	PC1	PC2
Cognition	Trainability	0.898	-0.114
Intelligence	Stubbornness	0.894	-0.190
Cognition	Ease at handling	0.889	-0.045
Intelligence	Memory	0.888	-0.117
Cognition	Cooperation	0.883	-0.111
Cognition	Emotional stability	0.861	-0.109
Intelligence	Docility	0.860	-0.047
Intelligence	Concentration	0.851	-0.073
Intelligence	Curiosity	0.753	-0.085
Cognition	Dependence	0.727	0.075
Cognition	Perseverance	0.711	0.400
Cognition	Get in/out of stables	0.590	0.426
Intelligence	Alertness	0.210	0.875
Eigen value		8.162	1.216
% Variance explained		62.781	9.357

The loadings and percentage of variance explained for each principal component (PC) with an eigen value > 1 are shown. Loadings > 0.6 are in bold.

first principal component (PC1) had strong positive loadings for all the cognitive processes studied, suggesting that donkeys scoring high on this factor show signs that may be indicative of better cognitive performance. The PC1 explained 62.78% of the cognitive variation. The second principal component (PC2) had weak negative loadings for all cognitive processes except for alertness and perseverance, and they only explained a 9.36% of the cognitive variation. We show a summary of the results for the PCA of the 300 donkeys assessed in [Table 3](#).

Genetic parameter assessment

For the studied variables, the highest estimate of additive genetic variance was obtained for stubbornness, which also accounted for the highest phenotypic variance ([Table 4](#)), whereas the lowest additive genetic variance estimates were obtained for alertness and perseverance.

We show estimates for variance components for all cognitive- and intelligence-related traits in [Table 4](#). For all estimates of h^2 , the SE was 0.01, indicating the high accuracy of the estimated parameters.

We show genetic and phenotypic correlations and heritability estimates for all the cognitive processes in [Table 4](#). Our estimated heritabilities ranged from 0.06 for dependence to 0.38 for the ability of the donkeys to enter or leave their stables. Phenotypic correlations (r_p) among all the seven general cognitive process-related or six specific cognitive process intelligence-associated traits were positive and from low to strong, with 0.12 (of alertness with dependence) being the lowest and 0.81 the strongest correlation (between memory and trainability) ([Table 4](#)). Genetic correlations (r_G) were generally positive and ranged from 0.11 to 0.97. However, all the correlations between alertness and the rest of traits except for those with dependence, emotional stability, perseverance, and the ability to get in/out stables were negative and from low to strong (–0.35 to –0.85), which were the lowest ones as well. Overall, the poorest correlation both phenotypically and genetically was obtained for alertness, whereas we got the strongest one for emotional stability ([Table 5](#)). The standard error for the phenotypic and genetic correlations was around 0.01 for all parameters ([Table 5](#)).

Predicted breeding values and descriptive statistics (“PBV Bayesian accuracies”)

The results for the estimates of PBVs ranged between –1.60 and 0.50. We show a summary of the descriptive statistics of the

breeding values obtained for each cognitive process sorted by sex in [Supplementary Table S3](#). The dispersion measures (“PBV Bayesian accuracies”) of the PBVs for each of the thirteen cognitive processes estimated after Gibbs sampling procedures are shown in [Supplementary Table S4](#).

Discussion

Our results suggest that donkeys' IQ similarly follows the gaussian distribution found in humans' IQ, although the curve is moderately deviated to the left ([Figures 2 and 3](#)). This is also shown by the polynomial regression equations (2nd order) and R squared (R^2 , determination coefficient or percent of explained variance) values that only differ by 0.0781 (7.81%). R^2 SD for donkeys' IQ was only 5.61% lower than that of humans' IQ, suggesting CIs may overlap.

Standard deviations are measured in the same units as the variables and hence directly determine the widths of CIs. [Nau \(2014\)](#) suggests that a 5% decrease in R^2 would increase the error SD by about 10% in relative terms. This begins to rise to the level of a perceptible widening in CIs, which means both IQs may distribute similarly with human IQ CIs being slightly narrower; hence humans' IQ values are more accurate.

Results indicate that the highest sample percentage (97%) that falls under 15–125 IQ in donkeys corresponds to a narrower IQ range in humans (70–130 IQ). However, when we extrapolated the results ([Figure 3](#)), we found more dissimilar sample percentages, that is, sharper differences between donkey individuals. There were donkeys that had IQ of 130 because of the nature of the cognitive processes. Some of these processes, such as getting in/out stables, were likely to be already significantly developed in very young animals, which slightly distorted the results for animals in the very lowest or highest IQ range.

In human psychometrics, individuals' scores are positively correlated across tasks assessing several cognitive domains, with a general factor typically accounting for 40%–50% of total variance ([Deary et al., 2007; Plomin, 2001](#)). We found from low to strong significant positive correlations between almost all cognitive processes, loading positively on the first component of PCA (PC1) and extracted with an eigen value >1 . PC1 captured almost 63% of donkeys' variance in cognitive performance, which has also been reported for primates for which g has proved to be responsible for 47%–60% of individual genetic variance in cognitive ability ([Locurto et al., 2013; Reader et al., 2011](#)) and about 55%–60% of individual variance in cognitive ability in mice ([Locurto and Scanlon, 1998](#)).

[Plomin \(2001\)](#) suggested that “cognitively complex” tasks present higher g loadings. Thus, low g loadings are consistent with the suggestion that certain cognitive processes may not be a good measure of animal cognitive ability ([Boogert et al., 2011](#)) because prior experience may have influenced their learning performance. In addition, the positive cognitive process intercorrelations could provide further evidence that animals' previous knowledge may not affect these abilities ([Boogert et al., 2011](#)). Our findings are consistent with those by [Woodley Of Menie et al. \(2015\)](#) on the fact that those cognitive abilities being more g-loaded would be more heritable and present larger additive genetic and phenotypic variance values ([Tables 2 and 3](#)).

Heritabilities suggest cognitive processes are complexly and moderately inheritable in donkeys. Heritabilities are generally moderate and similar to those for cognitive processes in literature and slightly higher than similar processes' estimates reported in other species, even more, when we consider the low standard error (higher accuracy) obtained, considering the limited sample size. [Darst et al. \(2015\)](#) obtained similar heritability values of 0.10 to 0.64 (standard error of the mean = 0.12 to 0.15, respectively) for

Table 4
Estimated genetic (σ_a^2), phenotypic (σ_p^2), and residual (σ_e^2) variances for intelligence and general cognitive processes in Andalusian donkeys, obtained from univariate analyses

Cluster	Cognitive process	σ_a^2	σ_p^2	σ_e^2
Intelligence	Concentration	0.2574	0.9022	0.6448
	Curiosity	0.1218	0.7636	0.6418
	Memory	0.0487	0.7012	0.6525
	Stubbornness	0.1537	1.1456	0.9919
	Docility	0.0856	0.7103	0.6247
	Alertness	0.0617	0.3041	0.2424
General cognition	Dependence	0.1806	0.8523	0.6717
	Trainability	0.1845	0.8753	0.6908
	Cooperation	0.0815	0.8057	0.7242
	Emotional stability	0.1304	0.6973	0.5669
	Perseverance	0.0534	0.5298	0.4764
	Get in/out of stables	0.1882	0.4949	0.3067
	Ease at handling	0.0874	0.8925	0.8049

Table 5 Estimated heritabilities ($h^2 \pm SE$) (diagonal), phenotypic ($r_P \pm SE$) (above diagonal), and genetic correlations ($r_C \pm SE$) (below diagonal) for intelligence and general cognitive processes in Andalusian donkeys

Cognitive process	Intelligence cluster					General cognition cluster					Ease at handling	
	Concentration	Curiosity	Memory	Stubbornness	Docility	Alertness	Dependence	Trainability	Cooperation	Emotional stability		Perseverance
Intelligence cluster												
Concentration	0.28 ± 0.01	0.51 ± 0.01	0.68 ± 0.01	0.70 ± 0.01	0.56 ± 0.01	0.37 ± 0.01	0.40 ± 0.01	0.70 ± 0.01	0.61 ± 0.01	0.54 ± 0.01	0.51 ± 0.01	0.32 ± 0.01
Curiosity	0.87 ± 0.01	0.16 ± 0.01	0.67 ± 0.01	0.60 ± 0.01	0.52 ± 0.01	0.35 ± 0.01	0.42 ± 0.01	0.63 ± 0.01	0.52 ± 0.01	0.48 ± 0.01	0.46 ± 0.01	0.56 ± 0.01
Memory	0.88 ± 0.01	0.60 ± 0.01	0.06 ± 0.01	0.74 ± 0.01	0.66 ± 0.01	0.17 ± 0.01	0.45 ± 0.01	0.81 ± 0.01	0.72 ± 0.01	0.62 ± 0.01	0.51 ± 0.01	0.50 ± 0.01
Stubbornness	0.69 ± 0.01	0.69 ± 0.01	0.64 ± 0.01	0.13 ± 0.01	0.73 ± 0.01	0.17 ± 0.01	0.34 ± 0.01	0.73 ± 0.01	0.71 ± 0.01	0.72 ± 0.01	0.48 ± 0.01	0.39 ± 0.01
Docility	0.87 ± 0.01	0.50 ± 0.01	0.54 ± 0.01	0.72 ± 0.01	0.22 ± 0.01	0.31 ± 0.01	0.32 ± 0.01	0.73 ± 0.01	0.65 ± 0.01	0.62 ± 0.01	0.42 ± 0.01	0.48 ± 0.01
Alertness	-0.59 ± 0.01	-0.85 ± 0.01	-0.70 ± 0.01	-0.71 ± 0.01	-0.54 ± 0.01	0.20 ± 0.01	0.12 ± 0.01	0.24 ± 0.01	0.17 ± 0.01	0.62 ± 0.01	0.39 ± 0.01	0.45 ± 0.01
General cognition cluster												
Dependence	0.92 ± 0.01	0.80 ± 0.01	0.87 ± 0.01	0.97 ± 0.01	0.89 ± 0.01	0.63 ± 0.01	0.21 ± 0.01	0.47 ± 0.01	0.47 ± 0.01	0.37 ± 0.01	0.43 ± 0.01	0.35 ± 0.01
Trainability	0.84 ± 0.01	0.82 ± 0.01	0.63 ± 0.01	0.83 ± 0.01	0.77 ± 0.01	-0.35 ± 0.01	0.93 ± 0.01	0.20 ± 0.01	0.65 ± 0.01	0.65 ± 0.01	0.46 ± 0.01	0.38 ± 0.01
Cooperation	0.89 ± 0.01	0.67 ± 0.01	0.64 ± 0.01	0.71 ± 0.01	0.59 ± 0.01	-0.46 ± 0.01	0.94 ± 0.01	0.86 ± 0.01	0.10 ± 0.01	0.64 ± 0.01	0.45 ± 0.01	0.39 ± 0.01
Emotional stability	0.92 ± 0.01	0.87 ± 0.01	0.65 ± 0.01	0.76 ± 0.01	0.61 ± 0.01	0.61 ± 0.01	0.87 ± 0.01	0.88 ± 0.01	0.67 ± 0.01	0.18 ± 0.01	0.46 ± 0.01	0.48 ± 0.01
Perseverance	0.62 ± 0.01	-0.18 ± 0.01	0.54 ± 0.01	0.50 ± 0.01	0.66 ± 0.01	0.50 ± 0.01	0.86 ± 0.01	0.80 ± 0.01	0.66 ± 0.01	0.61 ± 0.01	0.10 ± 0.01	0.40 ± 0.01
Get in/out of stables	0.49 ± 0.01	-0.50 ± 0.01	-0.42 ± 0.01	0.66 ± 0.01	-0.29 ± 0.01	0.07 ± 0.01	0.94 ± 0.01	0.11 ± 0.01	0.86 ± 0.01	-0.20 ± 0.01	0.71 ± 0.01	0.38 ± 0.01
Ease at handling	0.85 ± 0.01	0.49 ± 0.01	0.58 ± 0.01	0.59 ± 0.01	0.82 ± 0.01	-0.64 ± 0.01	0.94 ± 0.01	0.78 ± 0.01	0.77 ± 0.01	0.63 ± 0.01	0.80 ± 0.01	-0.64 ± 0.01

cognitive traits in human siblings with a parental history of Alzheimer's disease.

The only existing animal examples are those in mice by Galsworthy et al. (2005), who reported a heritability upper limit value ranging from 0.34 to 0.42. The PCA of thirteen cognitive traits carried out in the study by Hopkins et al. (2014) reported heritability values for g in chimpanzees of 0.012 to 0.538. This value remarkably improved after retesting the animals for two consecutive years (0.624 ± 0.242), suggesting that repeated measures may considerably improve the results obtained. This value was noticeably higher for h^2 and had a much higher standard error than our results did, but it is a controlled, laboratory study. Early attempts aiming at clarifying behavioral hereditary and additive components involving interaction factors (sex, age, breed, and handling conditions) suggest that, even with little environmental variation, individual genetic variation occurs (French, 1993; Hausberger et al., 2004; Wolff and Hausberger, 1996).

The low standard error in the heritabilities and correlations addresses the efficiency of the model used to study the genetic background of cognitive processes. Low to moderate heritabilities and high standard errors cited in the literature suggest that scientists are unable to infer accurate and suitable models to study the genetic fraction of total variation in behavioral traits.

The negative genetic correlation between alertness and most of the traits measured reflects the pattern of donkey behavior where extremely alert donkeys are not prone to be curious about external stimuli and unlikely to approach these stimuli. These donkeys were also difficult to handle or educate, uncooperative, less likely to concentrate and memorize the task introduced, and tended to display freezing coping strategies as highlighted by the negative correlations with stubbornness and docility. These values suggested that alertness is an independent trait (Table 3).

A negative genetic correlation between a pair of traits that holds a positive phenotypical correlation, for example, alertness with other cognitive processes (Table 5), has traditionally been attributed to countervailing environmental effects to which the animal adapts (Sgro and Hoffmann, 2004). Behavioral plasticity (Mery and Burns, 2010) accounts for such ability of organisms to change their behavior as a result of the exposure to certain stimuli. In this way, training, learning, or education can condition the expression of specific cognitive processes translating into phenotypical changes that differ from the genetic basis underlying.

A high phenotypic correlation linked to a high underlying genetic correlation enables the successful selection of the individuals with strong concentration skills while visually selecting for those animals that display better memory skills, are more stubborn, more easily trainable, more willing to cooperate and easier to handle. By contrast, if we aimed at selecting for more curious donkeys, we may only choose those displaying better memorizing skills, stubborn, and easier to train individuals. When selecting for donkeys for their memorizing skills, we indirectly select for individuals who concentrate easily, that are more curious, more stubborn, more docile, more easily trainable, more cooperative, more emotionally stable, and easier to handle.

While phenotypically selecting for stubborn animals, we may genetically select for animals that concentrate better, are more curious, have better memorizing skills, are more docile, cooperative, and easier to train and handle. Animals more easily engaging an alertness status will be less curious as well, both from a genetic and phenotypic perspective; thus, we should promote indirect selection strategies to select for one of both.

The low to moderate genetic correlations for dependence toward the owner with the rest of processes suggest that it is not a good criterion to follow to visually select donkeys for any other cognitive ability. However, more trainable and cooperative animals

will genetically be more prone to concentrate better, be more curious, have better memorizing skills, be more stubborn and docile. Moreover, the more stubborn the donkeys are, the more emotionally stable they are. Perseverance has no quantitatively important correlations and is not useful in the selection of other cognitive processes.

The ease at which animals enter their stables or leave them is moderately related to how stubborn the animal is. This evaluation may be affected by the nature of donkeys where freezing, avoidance of potentially stressing factors and return to a safe place are preferred behaviors. Ease of trainability in these donkeys correlated with cooperation, ease of concentration, and docility. The correlations we have found suggest remarkable synergism between most of the cognitive processes, as reported in chimpanzees (Hopkins et al., 2014). Visscher et al. (2008) reported a 0.5 to 0.8 human IQ heritability range, attributing the IQ-related traits' moderate-to-high standard error to the narrow range of sibling identity by descent.

From this finding, we can infer the fact that although the genes controlling for some behavioral traits may be topographically close or these traits may be features of the same cognitive process (enabling a simultaneous selection for both), some behavioral traits may be controlled by genes located at different loci or should be attributed to very distant cognitive processes (compelling to carry out an inverse selection strategy). Therefore, adding more data to the sample may reveal more reliable and independent personality components with higher heritabilities and may help to outline the relationships established between traits. Some traits may be under strong genetic control, but the particular population studied may have no genetic variation as a result of selection, also resulting in low heritability values. The values for additive variance enable the selection of individuals according to their cognitive abilities. Donkeys that may present a better cognitive development may potentially make the most of the elements present in their environments as well as may make educational or training plans easier and more effective, both regarding the money expended and the time devoted by a trainer/educator to get the donkey achieving the progress intended, and hence are more profitable.

Although we may be able to collaterally assess cognitive processes developed during the fulfillment of standardized tests, there are drawbacks. For instance, the likelihood of measuring a superficial behavior component, other behavioral elements, or the possibility of testing the owner's ability to educate donkeys instead of specific traits may translate into the moderate heritability values and standard errors found.

The use of well-defined and objective criteria assessed through proper standardized tests by a few well-trained judges reports typically much higher heritabilities. High correlations may suggest such skills may have been split into too numerous pieces or overlapping among cognitive traits involving more than one cognitive process and the cognitive process themselves individually. Therefore, reanalyzing data may reveal more reliable and independent personality components with higher heritabilities. Still, our results provide some of the first evidence that an analogous factor to human *g* may underpin cognitive performance in donkeys and account for a similar distribution in the human population.

Conclusions

Our results suggest that donkeys could be considered somehow intelligent animals when comparatively scoring them based on an analogous human scale. However, we do not intend to assert that some donkeys may account for a higher IQ than humans compared through the same scale. The cognitive processes and methods to score them widely differ from one species to another. Furthermore,

the more complex the cognitive development of the species being tested is, the more complex these methods should be (Gómez, 2005). However, a remarkable variation among donkeys is found, that is, there are donkeys which are more intelligent than others, and the present methodology enables quantifying such differences. The remarkably similar phenotypical distribution and inheritance patterns described in asses [compared to birds (Shaw et al., 2015), or other mammals (Hopkins et al., 2014), including humans (Hunt, 2010; Mortensen et al., 2005)] may suggest intelligence could be ascribed to a similar scientific background or even be supported by a similar genetic structure to the one widely studied in humans. Such finding lays the basis for future research to deepen in the field of animal cognition. Our results suggest that donkey's cognition heritable mechanisms may be attributed to human's similar genetic background. This study opens the door to selection and breeding for better cognitively performing animal generations. Our methodology comprises a novel approach to the animal intelligence controversy, using a standard human-applied method to score individual intelligence quotient.

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Ethical considerations

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All farms included in the study followed specific codes of good practices for equids and particularly donkeys, and therefore, the animals received humane care in compliance with the national guidelines for the care and use of laboratory and farm animals in research. The Spanish Ministry of Economy and Competitiveness through the Royal Decree-Law 53/2013 and its credited entity, the Ethics Committee of Animal Experimentation from the University of Córdoba, permitted the application of the protocols present in this study as cited in the 5th section of its 2nd article, as the animals assessed were used for credited zootechnical use. This national decree follows the European Union Directive 2010/63/UE, from the 22nd of September 2010.

Conflict of interest

The authors declare that they have no conflict of interest.

Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jveb.2019.06.007>.

References

- Alkhateeb-Shehadeh, H., 2008. Donkeys and mules in Arabic Veterinary Sources from the Mamluk Period (7th–10th/13th–16th Century). *Al-Masaq* 20, 207–214.
- Anderson, J.R., Bucher, B., Chijiwa, H., Kuroshima, H., Takimoto, A., Fujita, K., 2017. Third-party social evaluations of humans by monkeys and dogs. *Neurosci. Biobehav. Rev.* 82, 95–109.

- Bar-Oz, G., Nahshoni, P., Motro, H., Oren, E.D., 2013. Symbolic metal bit and saddlebag fastenings in a middle bronze age donkey burial. *PLoS One* 8, e58648.
- Baragli, P., Paoletti, E., Vitale, V., Sighieri, C., 2011. Looking in the correct location for a hidden object: brief note about the memory of donkeys (*Equus asinus*). *Ethol. Ecol. Evol.* 23, 187–192.
- Boogert, N.J., Anderson, R.C., Peters, S., Searcy, W.A., Nowicki, S., 2011. Song repertoire size in male song sparrows correlates with detour reaching, but not with other cognitive measures. *Anim. Behav.* 81, 1209–1216.
- Borioni, N., Marinaro, P., Celestini, S., Del Sole, F., Magro, R., Zoppi, D., Mattei, F., Dall'Armi, V., Mazzarella, F., Cesario, A., 2012. Effect of equestrian therapy and onotherapy in physical and psycho-social performances of adults with intellectual disability: a preliminary study of evaluation tools based on the ICF classification. *Disabil. Rehabil.* 34, 279–287.
- Bough, J., 2010. The mirror has two faces: contradictory reflections of donkeys in Western literature from Lucius to Balthazar. *Animals* 1, 56–68.
- Buzzichelli, S., Marzola, E., Amianto, F., Fassino, S., Abbate-Daga, G., 2018. Perfectionism and cognitive rigidity in anorexia nervosa: is there an association? *Eur. Eat. Disord. Rev.* 26, 360–366.
- Corballis, M.C., 2007. Recursion, language, and starlings. *Cogn. Sci.* 31, 697–704.
- Coutlee, C.G., Huettel, S.A., 2012. The functional neuroanatomy of decision making: prefrontal control of thought and action. *Brain Res* 1428, 3–12.
- Darst, B.F., Kosciak, R.L., Hermann, B.P., La Rue, A., Sager, M.A., Johnson, S.C., Engelman, C.D., 2015. Heritability of cognitive traits among siblings with a parental history of Alzheimer's disease. *J. Alzheimers Dis.* 45, 1149–1155.
- Deary, I.J., Irwing, P., Der, G., Bates, T.C., 2007. Brother–sister differences in the g factor in intelligence: analysis of full, opposite-sex siblings from the NLSY1979. *Intelligence* 35, 451–456.
- Deary, I.J., Penke, L., Johnson, W., 2010. The neuroscience of human intelligence differences. *Nat. Rev. Neurosci.* 11, 201.
- Dennett, D.C., 1994. The role of language in intelligence. In: Khalifa, J. (Ed.), *What Is Intelligence?* Cambridge University Press, Cambridge, p. 207.
- DeThorne, L.S., Schaefer, B.A., 2004. A guide to child nonverbal IQ measures. *Am. J. Speech Lang. Pathol.* 13, 275–290.
- Estaji, A., Nakhavali, F., 2011. Semantic derogation in Persian animal proverbs. *TPLS* 1, 1213–1217.
- Eysenck, H., 2018. *Intelligence: A New Look*. Routledge, New York, NY, p. 227.
- Folkman, S., Lazarus, R.S., Dunkel-Schetter, C., DeLongis, A., Gruen, R.J., 1986. Dynamics of a stressful encounter: cognitive appraisal, coping, and encounter outcomes. *J. Pers. Soc. Psychol.* 50, 992.
- Frick, P.J., Barry, C.T., Kamphaus, R.W., 2010. *Clinical Assessment of Child and Adolescent Personality and Behavior*. Springer, University of New Orleans, New Orleans, LA, p. 512.
- French, J.M., 1993. Assessment of donkey temperament and the influence of home environment. *Appl. Anim. Behav. Sci.* 36, 249–257.
- Galsworthy, M.J., Paya-Cano, J.L., Liu, L., Monleón, S., Gregoryan, G., Fernandes, C., Schalkwyk, L.C., Plomin, R., 2005. Assessing reliability, heritability and general cognitive ability in a battery of cognitive tasks for laboratory mice. *Behav. Genet.* 35, 675–692.
- Gerrig, R.J., Zimbardo, P.G., 2002. *American Psychological Association: Glossary of Psychological Terms*. Pearson Education, Education, Incorporated (COR), Washington. Available at: <https://dictionary.apa.org/mental-age>. Accessed May 18, 2019.
- Gómez, J.C., 2005. Species comparative studies and cognitive development. *Trends Cogn. Sci.* 9, 118–125.
- Goshen, I., Yirmiya, R.A.Z., 2007. The role of pro-inflammatory cytokines in memory processes and neural plasticity. In: Ader, R. (Ed.), *Psychoneuroimmunology*. Academic Press, Burlington, MA, pp. 337–377.
- Gottfredson, L.S., 2009. Logical fallacies used to dismiss the evidence on intelligence testing. In: Phelps, R.P. (Ed.), *Correcting Fallacies about Educational and Psychological Testing*. American Psychological Association, Washington, DC, pp. 11–65.
- Gregory, J., 2007. Donkeys and the equine hierarchy in archaic Greek literature. *Class. J.* 1, 193–212.
- Hausberger, M., 2002. Selection and Genetics of Behaviour of Horses. Presented at the Dorothy Russell Havemeyer Foundation 2nd Workshop, Horse Behavior and Welfare, 13rd–16th June, Hölar, 2002. Iceland.
- Hausberger, M., Bruderer, C., Le Scolan, N., Pierre, J.-S., 2004. Interplay between environmental and genetic factors in temperament/personality traits in horses (*Equus caballus*). *J. Comp. Psychol.* 118, 434–446.
- Herrmann, E., Call, J., 2012. Are there geniuses among the apes? *Phil. Trans. R. Soc. B* 367, 2753–2761.
- Hofmann, S.G., 2008. Cognitive processes during fear acquisition and extinction in animals and humans: implications for exposure therapy of anxiety disorders. *Clin. Psychol. Rev.* 28, 199–210.
- Hopkins, W.D., Russell, J.L., Schaeffer, J., 2014. Chimpanzee (*Pan troglodytes*) intelligence is heritable. *Curr. Biol.* 24, 1649–1652.
- Horowitz, A., 2014. *Domestic Dog Cognition and Behavior: The Scientific Study of Canis familiaris*. Springer Berlin Heidelberg, Berlin, Germany, p. 274.
- Hunt, E., 2010. *Human Intelligence*. Cambridge University Press, Cambridge, UK, p. 532.
- Kamphaus, R.W., Frick, P.J., 2005. *Clinical Assessment of Child and Adolescent Personality and Behavior*. Springer Science & Business Media, New York, NY, p. 486.
- Kaufman, A.S., 2018. *Contemporary Intellectual Assessment: Theories, Tests, and Issues*. Guilford Publications, New York, NY, p. 926.
- Kidd, C., Hayden, B.Y., 2015. The psychology and neuroscience of curiosity. *Neuron* 88, 449–460.
- Lazarus, R.S., Folkman, S., 1984. *Stress, Appraisal, and Coping*. Springer Publishing Company, New York, NY, p. 456.
- Littenberg, R., Tulkin, S.R., Kagan, J., 1971. Cognitive components of separation anxiety. *Dev. Psychol.* 4, 387.
- Locurto, C., Dillon, L., Collins, M., Conway, M., Cunningham, K., 2013. Implicit chaining in cotton-top tamarins (*Saguinus oedipus*) with elements equated for probability of reinforcement. *Anim. Cogn.* 16, 611–625.
- Locurto, C., Scanlon, C., 1998. Individual differences and a spatial learning factor in two strains of mice (*Mus musculus*). *J. Comp. Psychol.* 112, 344.
- Matzel, L.D., Sauer, B., 2017. IQ. In: Vonk, J., Shackelford, T.K. (Eds.), *Encyclopedia of Animal Cognition and Behavior*. Springer International, Department of Psychology, Rutgers University, Piscataway, NJ.
- Mery, F., Burns, J.G., 2010. Behavioural plasticity: an interaction between evolution and experience. *Evol. Ecol.* 24, 571–583.
- Miklósi, A., 2015. *Dog Behaviour, Evolution, and Cognition*. Oxford University Press, Oxford, UK, p. 400.
- Miklósi, Á., Kubinyi, E., 2016. Current trends in canine problem-solving and cognition. *Curr. Dir. Psychol. Sci.* 25, 300–306.
- Momozawa, Y., Kusunose, R., Kikusui, T., Takeuchi, Y., Mori, Y., 2005a. Assessment of equine temperament questionnaire by comparing factor structure between two separate surveys. *Appl. Anim. Behav. Sci.* 92, 77–84.
- Momozawa, Y., Takeuchi, Y., Kusunose, R., Kikusui, T., Mori, Y., 2005b. Association between equine temperament and polymorphisms in dopamine D4 receptor gene. *Mamm. Genome* 16, 538–544.
- Moran, A., 2011. 22 - Attention. In: Collins, D., Button, A., Richards, H. (Eds.), *Performance Psychology*. Churchill Livingstone, Edinburgh, pp. 319–335.
- Mortensen, E.L., Sørensen, H.J., Jensen, H.H., Reinisch, J.M., Mednick, S.A., 2005. IQ and mental disorder in young men. *Br. J. Psychiatry* 187, 407–415.
- Murphy, C.P., Jackson, R.C., Roca, A., Williams, A.M., 2015. Cognitive processes underlying anticipation in a context-oriented task. *J. Sport Exerc. Psychol.* 37, S53.
- Namikawa, J., Nishimoto, R., Arie, H., Tani, J., 2013. Synthetic Approach to Understanding Meta-Level Cognition of Predictability in Generating Cooperative Behavior, *Advances in Cognitive Neurodynamics (III)*. Springer Nature, Dordrecht, The Netherlands, pp. 615–621.
- Nau, R., 2014. *Notes on Linear Regression Analysis*. Fuqua School of Business, Duke University. Available at: http://people.duke.edu/~rnau/Notes_on_linear_regression_analysis-Robert_Nau.pdf. Accessed January 30, 2019.
- Navas, F.J., Delgado, J.V., Vargas, J., 2016. Current Donkey Production and Functionality: Relationships with Humans. Book 1. UcoPress, Córdoba, Spain, p. 779.
- Navas, F.J., Jordana, J., León, J.M., Arando, A., Pizarro, G., McLean, A.K., Delgado, J.V., 2017a. Measuring and modeling for the assessment of the genetic background behind cognitive processes in donkeys. *Res. Vet. Sci.* 113, 105–114.
- Navas, F.J., Jordana, J., León, J.M., Barba, C., Delgado, J.V., 2017b. A model to infer the demographic structure evolution of endangered donkey populations. *Animal* 11, 2129–2138.
- Navas, F.J., Jordana, J., León, J.M., McLean, A.K., Pizarro, G., Delgado, J.V., 2018. Genetic parameter estimation and implementation of the genetic evaluation for gaits in a breeding program for assisted-therapy in donkeys. *Vet. Res. Commun.* 42, 101–110.
- Navas González, F., Jordana Vidal, J., Pizarro Inostroza, G., Arando Arbulu, A., Delgado Bermejo, J., 2018a. Can donkey behavior and cognition be used to trace back, explain, or forecast moon cycle and weather events? *Animals (Basel)* 8, 215.
- Navas González, F.J., Jordana Vidal, J., León Jurado, J.M., Arando Arbulu, A., McLean, A.K., Delgado Bermejo, J.V., 2018b. Genetic parameter and breeding value estimation of donkeys' problem-focused coping styles. *Behav. Processes* 153, 66–76.
- Oken, B.S., Salinsky, M.C., Elsas, S.M., 2006. Vigilance, alertness, or sustained attention: physiological basis and measurement. *J. Clin. Neurophysiol.* 117, 1885–1901.
- OpenStax, 2014. *Measuring intelligence*. In: learning, L. (Ed.), *Psychology*. Rice University, Houston, TX.
- Osthaus, B., Proops, L., Hocking, I., Burden, F., 2013. Spatial cognition and perseveration by horses, donkeys and mules in a simple A-not-B detour task. *Anim. Cogn.* 16, 301–305.
- Plomin, R., 1999. The genetics of g in human and mouse. *Physiol. Behav.* 67, 659–669.
- Plomin, R., 2001. The genetics of g in human and mouse. *Nat. Rev. Neurosci.* 2, 136–141.
- Premack, D., 2007. Human and animal cognition: continuity and discontinuity. *Proc. Natl. Acad. Sci. U. S. A.* 104, 13861–13867.
- Proops, L., Burden, F., Osthaus, B., 2009. Mule cognition: a case of hybrid vigour? *Anim. Cogn.* 12, 75–84.
- Proops, L., Burden, F., Osthaus, B., 2012. Social relations in a mixed group of mules, ponies and donkeys reflect differences in equid type. *Behav. Processes* 90, 337–342.
- Reader, S.M., Hager, Y., Laland, K.N., 2011. The evolution of primate general and cultural intelligence. *Philos. Trans. Royal Soc. B* 366, 1017–1027.
- Roca, A., Ford, P.R., McRobert, A.P., Williams, A.M., 2011. Identifying the processes underpinning anticipation and decision-making in a dynamic time-constrained task. *Cogn. Process* 12, 301–310.
- Rossel, S., Marshall, F., Peters, J., Pilgram, T., Adams, M.D., O'Connor, D., 2008. Domestication of the donkey: timing, processes, and indicators. *Proc. Natl. Acad. Sci. U. S. A.* 105, 3715–3720.
- Saklofske, D.H., Schoenberg, M.R., Nordstokke, D., Nelson, R.L., 2017. Intelligence quotient. In: Kreutzer, J., DeLuca, J., Caplan, B. (Eds.), *Encyclopedia of Clinical Neuropsychology*. Springer International Publishing, Cham, Switzerland, pp. 1–5.

- Secchi, D., Bardone, E., 2009. Super-docility in organizations: an evolutionary model. *Int. J. Organ. Theor. Behav.* 12, 339–379.
- Sgro, C.M., Hoffmann, A.A., 2004. Genetic correlations, tradeoffs and environmental variation. *Heredity* 93, 241–248.
- Sharp, H., Wuensch, K., Eppler, M., Harju, B., 2006. Narcissism, Empathy, and Attitudes Towards Animals. Paper Presented at the Spring Conference of the North Carolina Psychological Association and North Carolina Psychological Foundation, Charlotte, NC.
- Shaw, R.C., Boogert, N.J., Clayton, N.S., Burns, K.C., 2015. Wild psychometrics: evidence for 'general' cognitive performance in wild New Zealand robins, *Petroica longipes*. *Anim. Behav.* 109, 101–111.
- Smith, A., 2006. Cognitive empathy and emotional empathy in human behavior and evolution. *Psychol. Rec.* 56, 3–21.
- Sparrow, S.S., Davis, S.M., 2000. Recent advances in the assessment of intelligence and cognition. *J. Child Psychol. Psychiatry* 41, 117–131.
- Spearman, C., 1904. "General Intelligence" objectively determined and measured. *Am. J. Psychol.* 15, 201–292.
- Sternberg, R.J., 1981. Testing and cognitive psychology. *Am. Psychol.* 36, 1181.
- Sudekum Trotter, K., Baggerly, J.N., 2018. Equine-Assisted Mental Health Interventions: Harnessing Solutions to Common Problems. Routledge Howick Place, London, UK, p. 280.
- Taylor, N., Signal, T.D., 2005. Empathy and attitudes to animals. *Anthrozoös* 18, 18–27.
- University of Minnesota, 2015. 9.2. The social, cultural, and political aspects of intelligence. In: University of Minnesota Libraries (Ed.), Introduction to Psychology. Minnesota. Available at: <http://open.lib.umn.edu/intropsyc/chapter/9-2-the-social-cultural-and-political-aspects-of-intelligence/>. Accessed July 21, 2019.
- Van Tassell, C., Van Vleck, L., 1995. A Manual for Use of MTGSAM. A Set of Fortran Programs to Apply Gibbs Sampling to Animal Models for Variance Component Estimation. US Department of Agriculture, Agricultural Research Service. Available at: <https://aipl.arsusda.gov/software/mtgsam/manual.html>. Accessed July 21, 2019.
- Visscher, P.M., Hill, W.G., Wray, N.R., 2008. Heritability in the genomics era—concepts and misconceptions. *Nat. Rev. Genet.* 9, 255–266.
- Wang, Y., Ruhe, G., 2007. The cognitive process of decision making. *Int. J. Cognit. Informat. Nat. Intell.* 1, 73–85.
- Way, K.C., 2014. Donkeys in the biblical world: ceremony and symbol. *J. Evang. Theol. Soc.* 57, 416–418.
- Wilson, D.S., Timmel, J.J., Miller, R.R., 2004. Cognitive cooperation. *Hum. Nat.* 15, 225–250.
- Wolff, A., Hausberger, M., 1996. Learning and memorisation of two different tasks in horses: the effects of age, sex and sire. *Appl. Anim. Behav. Sci.* 46, 137–143.
- Woodley Of Menie, M.A., Fernandes, H.B.F., Hopkins, W.D., 2015. The more g-loaded, the more heritable, evolvable, and phenotypically variable: Homology with humans in chimpanzee cognitive abilities. *Intelligence* 50, 159–163.