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Characterizing the heritability of cognitive and behavioural traits across development in domestic dogs

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In humans, many behavioural and cognitive traits are moderately-to-highly heritable, with cognitive measures tending to increase in heritability over the lifespan, and personality measures tending to decrease in heritability. However, fewer studies have explored the heritability of analogous traits in non-human animals or the changes of these heritability estimates across development. We phenotyped 415 dog puppies and 520 adults—from the assistance dog organization Canine Companions—on the Dog Cognitive Development Battery. Scores across tasks were weakly intercorrelated, and we observed a wide range of estimated heritabilities. Using an animal model and the population pedigree, the most heritable traits in puppies involved looking to a human when spoken to ('human interest looking', h^2 = 0.32) and reactions to a novel object (h^2 = 0.56) and surprising events (h^2 = 0.61). Most heritability estimates remained relatively stable or decreased over development, although human interest looking time (h^2 = 0.36) and novel object reactions (h^2 = 0.31) remained moderately heritable in adults. Similar heritability estimates were found using a genomic-relatedness matrix in a subset of individuals (69% of puppies, 96% of adults). Our results address the psychological structure of individual differences early in dog development, characterize the extent to which these traits are heritable and available to selection, and demonstrate changes in heritability across dog development.

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1. Introduction

Phenotypes fall on a spectrum of genetic control, ranging from traits minimally influenced by genetics and mostly shaped by environmental factors, to traits in which variation is predominantly genetic in origin [1]. Although the role of genetic and environmental contributions to a given trait can vary across populations, environments and time, characterizing the extent to which variation is explained by genetic factors can inform expected responses to selection, theories about trait evolution, and genomic association research. In quantitative genetics, heritability refers to the proportion of phenotypic variation in a population that is explained by genetic factors [2]. Heritability is a requirement for evolution by natural selection, as phenotypes must be differentially passed down to the next generation to produce change over time [3]. This concept of heritability can be further decomposed into different types of genetic effects, but we are most often interested in narrow-sense heritability, the proportion of variation explained by 'additive' genetic effects, rather than dominance or epistatic interactions between alleles or loci. Narrow-sense heritability can be estimated in multiple ways by comparing the phenotypes of individuals with known relatedness, and these estimates are directly related to a phenotype's potential to respond to selection, as well as the statistical power required for genome-wide association studies [1,2]. Importantly, however, a trait can be under strong genetic control but have effectively no heritability under this definition, because of minimal variation within a population. An example of such a trait is the number of limbs that an animal possesses; this trait is genetically encoded, but any variation observed within a population is almost exclusively caused by environmental factors (e.g. trauma resulting in atrophy or amputation).

Highly heritable traits in humans include height [4,5] and eye colour [6,7], while learnt behaviours and preferences are generally less but still significantly heritable [8]. There are a number of theoretical reasons why behavioural traits might be less heritable than morphological traits, and instead more sensitive to environment and experience [9–12]. However, it has also been argued that this idea of behaviour exhibiting exceptional plasticity may be owing to a false perception of the comparative lack of plasticity in other traits [13,14]. Heritability has been most commonly studied in humans through twin studies, usually within so-called WEIRD (Western, Educated, Industrialized, Rich and Democratic) populations [15], with fewer than 1% of studies including data from either South America or Africa [8]. Since heritability estimates are specific to a given population, this is an important caveat to the state of our existing knowledge. Nevertheless, a meta-analysis of studies comparing monozygotic and dizygotic twins suggests that temperament and personality measures have heritabilities in the range of 0.2–0.4, which is somewhat lower than the mean across all measured traits ($h^2 = 0.49$) [8]. Efforts to estimate the contribution of shared environmental effects to temperament and personality measures have yielded a somewhat smaller average value ($c^2 = 0.17$) [8], although this is particularly challenging to disentangle in human studies.

Human 'general intelligence', usually measured by an intelligence quotient (IQ) test, has often been estimated to have higher heritability, up to 0.86 in white populations (reviewed in [16,17]); however, the roles of maternal and other environmental effects—including *in utero* [18], genotype–environment correlations exacerbated by social stratification [19] and genotype × environment interactions [20]—have been documented and may undermine the highest of these estimates. Nevertheless, IQ tends to be one of the most highly heritable cognitive and behavioural measures in the existing literature; for example, one study that estimated the heritability of cognitive abilities in the range of 0.73–0.85, also estimated the heritability of 'inspection time' (the stimulus duration required for accurate perception) at a more moderate 0.45 [21]. It is worth noting explicitly that: (i) IQ is a problematic concept that is frequently overinterpreted and misused [22,23]; and (ii) these high heritabilities have been misapplied to support eugenics agendas [24]. In addition to racist motivations and deeply problematic assumptions about the comparative desirability of certain traits as well as variation in traits, one reason for the latter is the mistaken idea that high heritabilities imply genetic loci with large effects that could be selected for easily and quickly [2]. Instead, heritabilities capture all of the additive genomic contributions to a trait, and extreme polygenicity and epistatic effects mean that selection on any one trait will also have effects on other traits. Furthermore, the heritability of IQ is itself dependent on environment, particularly socioeconomic status, with high heritabilities observed only among affluent populations and a much larger role for environmental effects observed in less affluent populations [25]. Despite the issues surrounding the interpretation of IQ tests and their (mis)applications—and in part because of them—findings of high heritabilities in humans motivate broader questions about the heritability of cognitive and behavioural traits in other species.

There have been a few forays into the study of cognitive and behavioural heritability in non-human animals, however this has been relatively understudied in most species [16,26]. General intelligence has been estimated to have a heritability of 0.53 in chimpanzees [27] and 0.40 in mice [28]. In chimpanzees, Hopkins *et al.* also explored the heritability of principal component scores summarizing performance on a cognitive battery, finding two significantly heritable components (spatial and social cognition) and two minimally heritable components (visual causality/tool use and auditory causality) [27]. In great tits, exploratory behaviour in both novel environment and novel object tests was moderately-to-highly heritable, depending on the population ($h^2_{laboratory} = 0.54$; $h^2_{wild} = 0.25$–0.33) [29]. In rhesus macaques, estimated heritabilities range from 0.36 for 'anxious temperament' [30] and 0.38 for behavioural inhibition to 0.91 for vigilance [31]. In dogs, both task-directed behaviour ($h^2 = 0.32$) and human-directed social interactions ($h^2 = 0.23$) during an unsolvable task have been found to be heritable [32]. Multiple studies in dogs have also used owner surveys to assess dog personality and behaviour, demonstrating moderate heritabilities in at least some traits, with considerable variation across traits ($h^2 = 0.0$–0.8) [33–36]. However, detailed studies across a wide range of cognitive and behavioural traits are generally lacking [16]. Furthermore, laboratory studies may systematically overestimate heritability if environmental variation is lower than in natural or naturalistic settings [29,37,38]. In one study of laboratory mice, general cognitive ability—measured using a battery of five learning tasks—was found to be highly heritable in a control population maintained under standard laboratory conditions ($h^2 = 0.55$); however, in mice exposed to novel and enriched environments for 16 days, the same general cognitive ability was found to be both much improved—by 0.44 standard deviations—and much less heritable ($h^2 = 0.15$) [38]. This result is concordant with the affluence finding in humans [25] in that heritability is dependent on environment, but discordant in the directionality of the result, perhaps owing to the conformity of non-enriched laboratory environments.

A more extensive examination of multiple traits in different domains of cognition and behaviour can provide insight into what aspects of behaviour are more or less genetically or environmentally shaped in particular populations or species. Furthermore, most heritability estimates either use individuals at different ages or focus on a single timepoint in development. However, we know that personality and behavioural traits are not static over the course of the lifetime, so how does heritability change over the lifespan? If heritability decreases over the lifespan, this may be because of environmental effects becoming more pronounced with time. This is perhaps the most intuitive hypothesis for behavioural traits, as experience, learning, and memory accumulate across an individual's lifespan. A decrease in heritability over development can also be attributed to the decreasing importance of genetic effects, for example through epigenetic processes silencing genes later in development [39]. When heritability increases over the lifespan, it is often interpreted as genetic factors becoming more important over time. This could arise when genetic effects become most pronounced during certain life stages, for example during puberty [39]. In both cases of increasing and decreasing heritability across time, positive feedback loops can reinforce either genetically or environmentally driven differences, causing individuals with different genetics or environments to diverge increasingly over time [20,40]. Of course, these explanations are not mutually exclusive, and may vary in their importance across traits, species and the lifespan [16,39–41].

Studies in humans suggest that the heritabilities of certain cognitive traits increase over the lifespan [39,40]. Specifically, although resemblances between both monozygotic and dizygotic twins tend to decrease after adolescence [8,40], this change tends to be larger for dizygotic twins than for monozygotic twins, resulting in heritability estimates that increase with age. Measures of general intelligence typically demonstrate increased heritability over time [21,39,40,42,43]. By contrast, personality traits often demonstrate decreased heritability over time, although it is somewhat unclear whether this is owing to the increased importance of the environment or increased noise in measurement [40,41]. Such changes in heritability estimates over the lifespan have been studied considerably less for phenotypes other than general intelligence or in non-human animals.

Dogs present an ideal opportunity to explore these questions because they are eager participants in a variety of cognitive and behavioural tasks, they exhibit considerable individual differences on these measures, and there are large populations of dogs with known pedigrees available for research. Furthermore, the dog genome is well documented, which will facilitate subsequent genomic studies aimed at identifying specific genetic contributions to heritable traits [44,45]. Past research demonstrated that a variety of behavioural traits measured by owner questionnaire [35] had relatively high among-breed heritabilities (mean $h^2 = 0.51$), ranging from non-social fear ($h^2 = 0.27$) to trainability ($h^2 = 0.77$), although heritability estimates for the same behavioural traits in single-breed analyses have been lower [33,46]. A similar analysis using the *Dognition.com* test battery and breed-average genetic data found two cognitive factors—interpreted as inhibitory control and sensitivity to human communication—that were relatively highly heritable across breeds, whereas two cognitive factors—interpreted as physical reasoning and memory—were also significantly heritable but with notably less variation explained by breed-average genetic variation [47]. Using novel owner-surveys and paired genetic samples, Morrill *et al.* found that most measured behavioural traits were also moderately heritable ($h^2 > 0.25$) [36]. This type of work has generally relied on owner report, community science, breed-average genetic data and/or variation across breeds. Furthermore, most of these studies have focused exclusively on adult dogs.

Past work establishing the Dog Cognitive Development Battery (DCDB) assessed a variety of cognitive and behavioural phenotypes in puppies and young adults, finding moderate stability over development for some traits [48,49]. Furthermore, a subset of social traits measured on this battery were found to be moderately-to-highly heritable in two-month-old puppies [50]. In the current study, we use the DCDB data from hundreds of dogs to (i) assess the psychological structure of individual differences in cognitive and behavioural traits in a population of domestic dogs, and (ii) estimate and compare the heritabilities of these phenotypes at two timepoints. To do this, we tested individuals from a pedigreed population on a battery of 15 cognitive and behavioural tasks at two months old and approximately two years old. We then explored the factor structure of individual differences and the heritability of phenotypic measures at both timepoints. Our results shed light on the psychological structure of individual differences early in dog development, the extent to which these cognitive and behavioural traits are heritable and therefore available to selection, and how these heritability estimates change across development in dogs.

2. Methods

2.1. Subjects

All study subjects ($n = 415$ puppies; $n = 520$ adults) were part of the breeding and training programme at Canine Companions®. The Canine Companions breeding programme produces approximately 900 puppies a year, trains them for various service dog roles, and places them with individuals with disabilities. This is a relatively closed breeding population, although outside breeders are regularly introduced to avoid inbreeding depression. Except for those outside breeders, all dogs in this population are born at or near the Canine Companions headquarters located in northern California, USA. Littermates are raised together for the first eight weeks of their lives, either in volunteer breeder-caretaker homes or in the Canine Companions Canine Early Development Center. At around eight weeks of age, all puppies then have veterinary checks at Canine Companions' headquarters before being placed with volunteer puppy raisers. During their time at headquarters, we conducted cognitive testing and biological sample collection on a subset of the population. Subjects were approximately 7–10 weeks old at this first timepoint of cognitive testing. After this, all puppies are placed in volunteer puppy-raiser homes across the country, with littermates raised apart, serving as a natural experiment that helps to disentangle genetic and environmental effects. At 1.5–2 years of age, dogs return for professional training to one of six regional campuses, located in northern California, southern California, Texas, Ohio, Florida and New York. In most cases, adult cognition testing was conducted soon after dogs returned to campus for professional training. At the puppy timepoint, we enrolled 1–2 litters per dam and 1–5 individuals per litter; our puppy sample included 224 females and 191 males. At the adult timepoint, we prioritized individuals tested as puppies ($n = 291$), as well as their parents—both the dam ($n = 130$) and sire ($n = 45$) of each puppy—although we also tested additional adults ($n = 54$). Our adult sample included 329 females and 191 males; the female bias among the adults is primarily owing to the inclusion of parent breeders, as the population has many more breeding dams than sires.

All individuals in this population are either Labrador retrievers, golden retrievers, or—most commonly—crosses between the two. However, the crosses are not all first- or second-generation crosses that are easily categorized; we therefore used the entire population pedigree to calculate each individual's per cent Labrador retriever ancestry and constructed three binned breed categories: mostly golden ancestry (0–33.3% Labrador), relatively even breed composition (33.3–66.7% Labrador), and mostly Labrador ancestry (66.7–100% Labrador). At the puppy timepoint, our sample included 308 individuals with mostly Labrador ancestry, 37 individuals with mostly golden ancestry and 70 individuals with approximately evenly mixed ancestry; at the adult time point, our sample included 380 mostly Labradors, 52 mostly goldens and 88 even mixes. This breed category was used as a covariate in all heritability models.

2.2. Pedigree

The population pedigree was summarized using tools from the R package *pedigree* (version 1.4.2) [51] and the completeness function from the package optiSel (version 2.0.9) [52]. The entire pedigree includes more than 26 000 individuals with a maximum depth of 16 generations. The 644 individuals in this study have an average generation depth of 12.5 ± 1.4 in the population pedigree; counting the individual as generation 0, mean completeness at generation 4 is 99%, with only 17 individuals having incomplete coverage of great-great-grandparents. Using the entire population pedigree, the mean coefficient of inbreeding for individuals in this study was 6%, although we note that this is undoubtedly an underestimate of inbreeding compared to genomic-based methods.

2.3. Dog Cognitive Development Battery

The DCDB is composed of various experimental cognitive and behavioural tasks designed to measure human-oriented social cognition, independent problem solving, memory processes, inhibitory control, perceptual discriminations and aspects of temperament (e.g. neophobia and recovery when exposed to novel objects and startling events). The tasks in this battery were primarily based on measures that have been associated with training outcomes in previous studies of assistance and explosive detection dogs [53–55]. These measures and methods have already been reported in both puppies and adults with a subset of the individuals included in this study [48–50].

In the current study, most dogs were tested as puppies and then again as adults early in training (n = 291), while the remaining individuals were tested only once (n = 124 puppies; n = 229 adults). At the puppy timepoint, subjects were tested at approximately 7–10 weeks of age (mean ± s.d. = 59 ± 5.5 days; median = 57; range = 51–73). At the adult timepoint, most dogs were tested at approximately 2 years old (median = 1.94 years), although in general the dams and sires were tested at older ages (n = 143 dogs tested at > 2.5 years). The DCDB was very similar across the two timepoints, with only a few alterations to the adult version (compared with the puppy version), the most significant being the removal of the vision pretest and the addition of one task (problem solving). The ethograms for video scoring of temperament tasks also differed slightly, resulting in somewhat different raw measures. For sample sizes and a brief description of each DCDB measure, see tables 1 and 2. For a longer description of each task and the experimental methods, see [56]; video examples of each task are also included as electronic supplementary material in [49].

All DCDB measures were reliable for data collected at both timepoints. For the puppy measures, there was high inter-rater agreement on both live-coded (Cohen's Kappa: mean = 0.93; Pearson's r: mean = 0.95) and video-coded (Cohen's Kappa: mean = 0.90; Pearson's r: mean = 0.95) measures. Raw reliability statistics for a subset of the puppy data are reported in Bray *et al.* [48]. Reliability was also excellent for adult measures with high inter-rater agreement on live-coded (Cohen's Kappa: mean = 0.97; Pearson's r: mean = 0.99) and video-coded (Cohen's Kappa: mean = 0.97; Pearson's r: mean = 0.97) measures. Raw reliability statistics for a subset of the data at this second timepoint are presented in Bray *et al.* [49].

2.4. Statistical analyses

2.4.1. Principal component analyses

While some of the DCDB tasks result in a straightforward, single measure (e.g. per cent of trials correct), other tasks included multiple measures, often requiring coding from video. For all tasks with multiple measures, we explored variable reduction using the *psych* package [57] in R version 4.1.3 [58], separately within each age group (puppy and adult timepoints). We first rank-normalized each measure, then conducted parallel analyses on the Pearson correlation matrices to determine whether a principal component

Table 1. Overview of cognitive and behavioural phenotypes and sample sizes (except temperament tasks, see table 2). (Sample sizes (*n*) are given as puppy/adult. OC, object choice; PC, principal component; C1, component 1; E, experimenter; DV, dependent variable.)

measure	*n*	description
retrieval score	415/519	structured game of fetch, scored on touching the ball, picking it up and number of retrievals. DV: average score (1–6) across two trials
cylinder—inhibitory control score	410/519	after learning path to retrieve food from side of opaque cylinder, apparatus is replaced with transparent cylinder. DV: number of test trials the dog retrieves the food from the open side, without first touching the cylinder
cylinder—detour C1	408/516	after inhibitory control test trials, the preferred side is blocked, and ability to access through the other side (detour) is assessed. DV: PC of score, latency and approach path
human interest—looking	397/520	E looks at dog and recites script using dog-directed speech. DV: average time subject looks at E's face across three trials
human interest—interaction	397/520	after dog-directed speech, E steps into the experimental area and pets the dog if they come within reach. DV: average time subject interacts with E across three trials
human interest—C1	397/-	DV: PC of human interest looking and interaction (equal loadings)
unsolvable task C1	415/515	subject learns to access food from container, then lid is locked on and dog has 30 s to attempt to access food or seek help from E. DV: PC of average time subject looks at E's face and average time physically interacting with the container across four trials (equal opposite loadings)
laterality—index C1	415/520	subject repeatedly steps up onto and then down off of a platform, and the first paw used is recorded. $[R - L] / [R + L] \times 100$. DV: PC of up and down steps (equal loadings)
laterality—strength C1	415/520	absolute value of laterality index. DV: PC of up and down steps (equal loadings)
warm-ups C1	380/518	OC: food visibly placed under one of two cups. Subject allowed to search immediately. DV: PC of trials to pass criterion across sessions, sign flipped for intuitive interpretation
spatial working memory C1	400/481	OC: food visibly placed under one of two cups. Subject allowed to search after time delay. DV: PC of per cent correct in 5 s and 10 s delays (puppies) or 20 s and 40 s delays (adults)
gesture: marker	407/516	OC: food placed (unseen) under one of two cups. E uses ostensive cues and places a wooden block next to the baited cup. DV: per cent of correct choices
gesture: pointing	402/518	OC: food placed (unseen) under one of two cups. E uses ostensive cues and points to baited cup using a static, contralateral pointing gesture with a gaze cue. DV: per cent of correct choices
auditory discrimination	413/519	OC: food dropped audibly into one of two bowls (while other bowl is false baited). DV: per cent of correct choices
visual discrimination	414/520	OC: food placed on one plate; dog shown both the baited plate and an empty plate before choosing. DV: per cent of correct choices, binarized into <100% versus 100%
odour discrimination C1	408/515	OC: two small rubber tubes, one baited. Subject is allowed to sniff both tubes before approaching and interacting for up to 20 s. DV: PC of first and last choice, time in proximity to each and total interaction with either
problem solving C1	-/520	dog attempts to extract food from two interactive puzzles. Productive engagement scored as a combination of trial completion and latency to solve. DV: PC of scores from both puzzles

Table 2. Overview of the two temperament phenotypes (novel object and surprising events), which are scored from video with behavioural ethograms, and sample sizes for each task. (Sample sizes (*n*) are given as puppy/adult. Principal component (PC) loadings for both tasks are shown in the electronic supplementary material, figures S1–S2. For both tasks, a single component (C1) was extracted to summarize the coded variation, and scores on this PC were used as the phenotypes for subsequent analysis. E, experimenter; DV, dependent variable.)

measure	*n*	description
novel object C1	415/519	subject is left alone in the testing area with one (puppy) or two (adult) robotic cat(s) for 2 min, after which E encourages the subject to approach the cat(s) and rewards them with food. DV: PC of ethogram coded from video (see the electronic supplementary material, figures S1 and S2). Interpretation: shy (−)/bold (+)
surprising events C1	408/516	subject is exposed to a series of events: sudden appearance (falling trash bag), looming object (opening umbrella), loud noise (shaking metal sheet). After each event, E encourages the subject to approach the object and rewards them with food. PC of ethogram including initial reaction, solo-approach, experimenter-encouraged approach and re-approach, and vocalizations. DV: PC of ethogram coded from video (see the electronic supplementary material, figures S1 and S2). Interpretation: shy (−)/bold (+)

reduction was warranted, and where at least one component was supported, a single component was extracted for each task. For laterality, we treated index (right versus left paw bias) and strength (magnitude of bias) separately, and for cylinder we treated the inhibitory control and detour (reversal) sections of the task separately, given the conceptual distinctness of each. For the human interest task, a principal component was supported in puppies but not adults, so we retained all measures to enable direct comparison across timepoints.

2.4.2. Exploratory factor analyses

To explore the relationships between measures in the DCDB, we conducted exploratory factor analyses using the *psych* package [57] in R version 4.1.3 [58], separately within each timepoint (puppy and adult). Only individuals with complete cognitive and behavioural data were used in these analyses (n = 348 puppies; n = 470 adults). We used parallel analysis to determine the number of factors indicated and then extracted the indicated number of factors using a varimax rotation.

2.4.3. Heritability analyses

All linear modelling was conducted in a Bayesian framework on a high-performance computing cluster using the *brms* package version 2.16.3 [59–61] in R version 4.2.2 [58]. All heritability models were specified with fixed effects for sex, breed category, experimenter and age at phenotyping. Sex was analysed as a binary variable, not considering neuter status, with females as the reference level. As described above, three breed categories were used: mostly Labrador ancestry, mostly golden ancestry, and approximately even mixes, with the mostly Labrador category used as the reference level. The experimenter was the primary person presenting choices, manipulating apparatuses and talking to the subject during DCDB testing. Because this was a multi-year, multi-site study, there were 11 experimenters for puppies and 14 experimenters for adults in this dataset. For analysis, we collapsed data for anyone who had experimented for fewer than 20 dogs into an 'other' category, which was the reference level; this resulted in nine experimenter levels for puppies and six for adults. Puppies were tested at approximately 7–10 weeks of age (mean ± s.d. = 59 ± 5.5 days; median = 57; range = 51–73). Adults were tested at a wider variety of ages, as discussed above, mostly around 2 years of age (mean ± s.d. = 2.5 ± 1.2; median = 1.9; range = 1.0–10.8 years). For puppies, we included a fixed effect for rearing location (breeder-caretaker home or Canine Early Development Center) and for adults we included a fixed effect for testing location (Canine Companions campus in northern or southern California). For fixed effects, we used weakly regularizing priors, normally distributed with a mean of 0 and s.d. of 1. Using an animal model, we estimated the genetic contribution to each trait using a relatedness matrix [62]. Visual discrimination was the only measure with insufficient match in the posterior predictive check, owing to a large proportion of individuals performing at ceiling (100% correct); we therefore discretized this phenotype into a binary measure (less than perfect performance versus perfect performance) and modelled it using a Bernoulli distribution with a logit link function. All other models used rank-normalized phenotypes and a Gaussian distribution.

Most studies of heritability have only pedigree information or genomic sequencing information available, and in the relatively rare instances that both are available, results are often discordant, emphasizing the importance of direct comparisons. In this study, we therefore estimated all heritabilities in two ways: using the pedigree-based relatedness matrix and using a genomic-relatedness matrix (GRM). The former method used Canine Companions' population pedigree to calculate relatedness between each pair of individuals based on relatedness coefficients (i.e. 1/2 for parents, children and full siblings) extrapolated to the entire population. The latter method used whole-genome sequences to infer relatedness using the kinship coefficient, calculated by the *relatedness2* function [63] in VCFtools [64], multiplied by two; the GRM analyses included somewhat fewer individuals ($n_{puppy} = 285$, 69% of pedigree sample; $n_{adult} = 501$, 96% of pedigree sample) owing to the availability of sequence data. The sequence data was obtained from whole-genome sequencing of DNA extracted from blood samples, resulting in 6 520 035 single nucleotide polymorphisms (SNPs). For an overview of the sample processing and sequencing, see the electronic supplementary material. The resulting GRM was not positive definite, so we used the *nearPD* function in the *R* package *Matrix* [65] to solve for the nearest positive definite matrix, which was then used in the GRM heritability models. We compared the relatedness matrices themselves using a Mantel test, implemented in the *vegan* package [66].

In both sets of analyses, the animal model partitions variance between genetic and environmental components, yielding narrow-sense heritability estimates; these estimates are theoretically indicative of additive genetic variance, although there may still be effects from dominance, epistasis and maternal effects [62] that we are unable to disentangle in the current study for a combination of statistical and practical reasons. All heritability models were run for 50 000 total iterations across four chains, with a thinning interval of 5, and warm-up of 1000. To minimize divergences (<5%), an adapt_delta of 0.999 was used. For all heritability results, we report the median heritability estimate from the posterior distribution and 95% credible intervals. We also ran null-models without a relatedness matrix, and for the pedigree-based analyses, we computed Bayes factors (BF) as an indicator of the support for the trait being heritable (electronic supplementary material, table S1); BFs above 10 are considered strong support for the model including the relatedness matrix, and thus for heritability of that trait.

3. Results

3.1. Principal component analyses

Principal component analysis (PCA) resulted in similar—but not identical—summary measures for puppies and adults. Components loaded by at least three measures are shown in the electronic supplementary material, figure S1 for puppies and figure S2 for adults. In particular, the temperament tasks were scored from video on complex ethograms, yet resulted in very similar patterns of loadings across time, with highly correlated loadings in puppies and adults (novel object: $r = 0.94$; surprising events $r = 0.88$). The similarity across timepoints increases the interpretability of comparisons across these timepoints.

3.2. Factor analyses

Exploratory factor analyses of the DCDB measures revealed minimal correlational structure. At both timepoints, three factors were indicated, with minimal added interpretability (electronic supplementary material, figure S3). Although this battery included multiple human-oriented social cognitive tasks, none of them loaded together significantly on a factor. For example, average looking time during human-interest and point-following were not correlated in either puppies ($r = -0.01$) or adults ($r = 0.06$), suggesting that performance on the point-following task is not simply explained by variation in general attention to a human experimenter. The two gesture tasks (pointing and marker) were also uncorrelated in both puppies ($r = 0.07$) and adults ($r = -0.005$). The highest correlations were observed for the two temperament tasks, novel object and surprising events, both of which are measured by principal component reductions that can be interpreted as shyness-boldness; nevertheless, performance on these two tasks was only moderately correlated at both timepoints ($r_{puppy} = 0.33$; $r_{adult} = 0.36$). Furthermore, in our factor analyses, the proportion of variance explained was 7% or less for every factor and the cumulative common variance explained 16% or less. Similar exploratory factor analyses using multiple measures per task did not reveal additional compelling factor structure (data not shown). We therefore proceeded

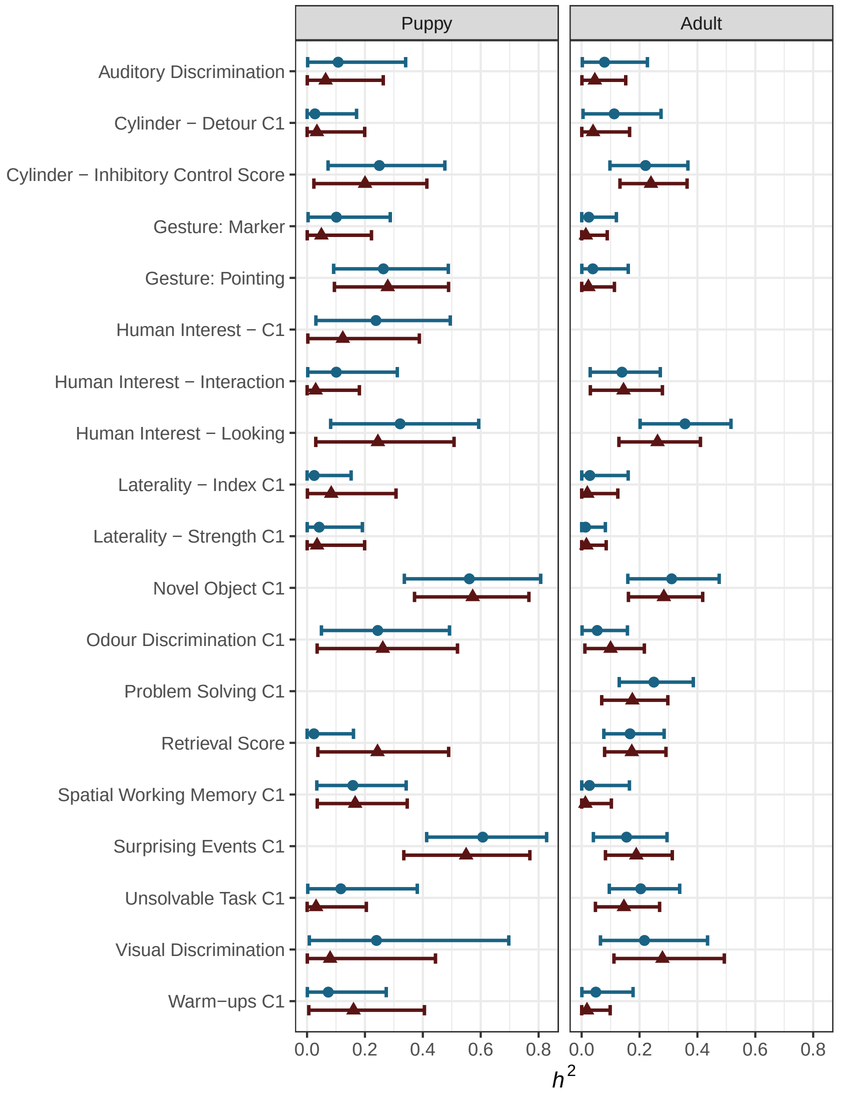

Figure 1. Estimated heritabilities of DCDB tasks at puppy (left) and adult (right) timepoints using the population pedigree (blue circles) and the genomic-relatedness matrix (maroon triangles). The points represent medians of the posterior distributions, with the error bars showing 95% credible intervals. Task names that include 'C1' denote phenotypes derived from PCA scores. Heritability estimates range from 0.01 to 0.61, with the highest heritabilities observed for novel object and surprising events in puppies and for human interest in adults.

with analyses of each task separately, using a single raw measure or principal component for each task, except where a second measure was theoretically motivated owing to conceptual distinctness and prior research. Specifically, the following tasks were represented by two measures: cylinder (sub-tasks for inhibitory control and detour reversal [67,68]), laterality (direction and strength [69,70]) and human interest (gaze and interaction during the distinct phases [71–74]).

3.3. Pedigree-based heritability estimates

We used the Canine Companions population pedigree and an animal model [62] to estimate the narrow-sense heritability of each phenotype from the DCDB among puppies and adults separately. Heritability estimates at the puppy timepoint ranged from 0.02 to 0.61, with a mean of 0.19 and median of 0.14 (figure 1). Heritability estimates at the adult timepoint ranged from 0.01 to 0.36, with a mean of 0.14 and median of 0.13 (figure 1). In general the heritability estimates decreased between the two timepoints, only increasing notably for retrieval, unsolvable task and cylinder detour (figure 2); however, all estimates except surprising events had overlapping credible intervals at the two timepoints.

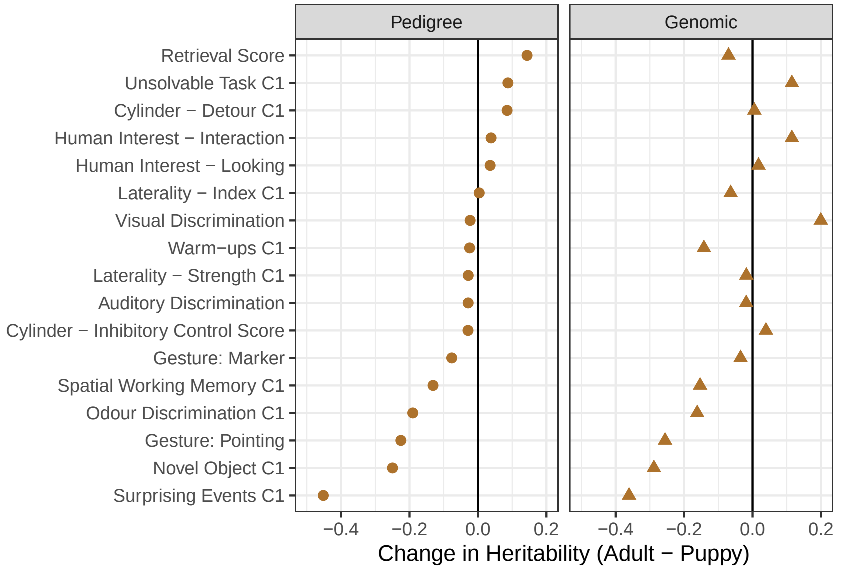

Figure 2. Changes in estimated heritabilities between timepoints (adult – puppy) from models that used a pedigree-based relatedness matrix (circles; left panel) or a genomic-relatedness matrix (triangles; right panel). The genomic-relatedness matrix was calculated from whole-genome sequencing conducted on a subset of individuals ($n = 285$ puppies, 501 adults) included in the pedigree-based analysis ($n = 415$ puppies; $n = 520$ adults). Task names that include 'C1' denote phenotypes derived from PCA scores. In both cases, the only change with non-overlapping credible intervals was for surprising events.

Among puppies, the two most highly heritable measures were from the two temperament tasks: novel object ($h^2 = 0.56$; $BF = 8.18 \times 10^5$) and surprising events ($h^2 = 0.61$; $BF = 1.21 \times 10^{10}$; figure 1). The most highly heritable trait in adults was looking time in the human interest task ($h^2 = 0.36$; $BF = 2239.79$; figure 1). Novel object was the second most highly heritable measure among adults, although the heritability estimate ($h^2 = 0.31$; $BF = 455.83$) was considerably lower than in puppies. The largest decrease in heritability across development was for the surprising events task (figure 2). In puppies, intermediately heritable traits included the social measures human interest looking time ($h^2 = 0.32$; $BF = 3.61$) and point-following ($h^2 = 0.26$; $BF = 11.78$), as well as inhibitory control ($h^2 = 0.25$; $BF = 5.27$). In adults, intermediately heritable traits included problem solving ($h^2 = 0.25$; $BF = 388.11$), inhibitory control ($h^2 = 0.22$; $BF = 37.68$) and visual discrimination ($h^2 = 0.22$; $BF = 13.66$), as well as retrieval ($h^2 = 0.17$; $BF = 85.41$), looking versus manipulation time on the unsolvable task ($h^2 = 0.20$; $BF = 92.97$) and looking time on the human interest task ($h^2 = 0.36$; $BF = 2239.79$). The other social tasks were minimally heritable at this timepoint (figure 1). Heritability estimates and BFs are provided in the electronic supplementary material, table S1. Estimates with lower credible intervals near zero and BFs of less than 1 are not significantly heritable.

3.4. Genomic-relatedness matrix-based heritability estimates

The heritability of a trait in a given population can be estimated through twin studies (common in humans), parent–offspring regression, using known relatedness among individuals from a population pedigree, or using genomic sequence data to calculate genomic relatedness. It is not uncommon for these different approaches to yield rather different results, raising a variety of both theoretical and methodological questions regarding the observed discrepancies; and directly comparable datasets are rare. Since we had sequence data available for a large proportion of individuals in this study (69% of puppies, 96% of adults), we compared two methods of heritability estimation: using the population pedigree—presented above—and a genomic-relatedness matrix (GRM). We fitted an identical set of models using a GRM for individuals with available sequence data. The two relatedness matrices were moderately-to-highly correlated (before conversion to nearest positive definite: Mantel $r = 0.676$; after conversion: Mantel $r = 0.745$). Heritability estimates changed only slightly when the GRM was used (median difference = 0.01; range = −0.22, 0.16; figure 1), and the results were highly correlated ($r_{all} = 0.88$; $r_{puppy} = 0.87$; $r_{adult} = 0.90$; figure 3). The largest differences (>0.1) were seen in the puppy estimates for human interest (C1), visual discrimination and retrieval.

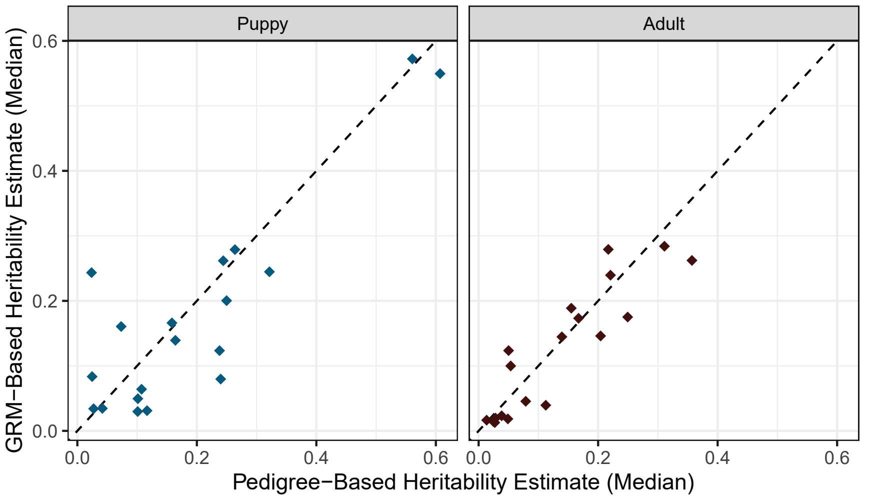

Figure 3. Correspondence between heritability estimates using a pedigree and a genomic-relatedness matrix (GRM) calculated from whole-genome sequencing data. The correlation across methods is high in both puppies ($r = 0.87$) and adults ($r = 0.90$). The GRM analysis includes a subset of the individuals in the pedigree analysis, based on sequence availability.

4. Discussion

In this study, our pedigree-based heritability estimates of cognitive and behavioural traits ranged from 0.02 to 0.61 in puppies and from 0.01 to 0.36 in adults, with most heritability estimates remaining relatively stable or decreasing from early life to young adulthood. Since strong selection reduces heritability by depleting genetic variation, traits with moderate observed heritability have presumably not been under strong recent selection in this population. Past studies of the heritability of cognitive and behavioural traits in dogs have produced heritability estimates of relatively similar magnitudes, with a wide range across traits [33–36,47,75,76], as have studies in other species [16]. Among-breed approaches using breed-average genetic relatedness have generally produced somewhat higher heritability estimates [35,47]. Using individual-level analyses and a sequence-based GRM, Morrill *et al.* demonstrated that most of their owner-survey-based behavioural traits were moderately heritable ($h^2 = 0.25$); they also found that retrieving ($h^2 = 0.525$) and human-oriented sociability ($h^2 = 0.673$) were particularly highly heritable behaviours [36]. These estimates are again much higher than observed here, although in our study the heritability of retrieval increases from early life to young adulthood. Since heritability estimates are population-specific, these differences are unsurprising, especially given the heterogeneity of other study populations compared to the Canine Companions population. It is also plausible that heritabilities of traits measured by owner surveys may be inflated because of human biases in breed perceptions [77], or conversely, owners may be better able to provide an average trait assessment than the context-specific snapshot provided by an experimental procedure at a single timepoint.

A number of studies have also implemented single-breed heritability analyses of behavioural traits in dogs. Our average heritabilities are similar to those in Hradecka *et al.*'s review and meta-analysis [75], although certain traits here exhibit higher heritabilities. Ilska *et al.* estimated the heritabilities of personality traits measured by the Canine Behavioral Assessment and Research Questionnaire (C-BARQ), an owner questionnaire, focusing on Labrador retrievers from the United Kingdom—including pet dogs, gun dogs and show dogs—all at least 2 years old [33]. The heritabilities reported by Ilska *et al.* range from 0.03 for owner-directed aggression to 0.38 for fetching, using a pedigree-based analysis; a similar analysis using a GRM found heritabilities ranging from 0 for attention and excitability to 0.31 for fear of noises. The magnitude of these heritability estimates are similar to those for DCDB phenotypes at the adult timepoint. However, Ilska *et al.* found generally lower heritabilities using the GRM than using the Kennel-Club pedigree [33], whereas we found minimal differences between the two approaches. One possible reason for this divergence is a different method of sampling the population, including many first-degree relatives in our study. Another potential explanation is that they used array-based SNP genotyping, with 108 829 autosomal markers after filtering criteria, while we used low coverage whole-genome sequencing and population-specific imputation with 6 520 035 SNPs. Friedrich *et al.* also examined the heritabilities of C-BARQ traits in German shepherds, finding somewhat lower heritabilities on average, with only 3 of

13 traits yielding heritability estimates above 0.1 in each analysis; the highest estimates were for human-directed playfulness ($h^2_{pedigree}$ = 0.23; h^2_{GRM} = 0.17), followed by non-social fear ($h^2_{pedigree}$ = 0.12; h^2_{GRM} = 0.16) [34]. More recently, Matsumoto *et al.* estimated the heritabilities of seven behavioural phenotypes using whole genome sequencing and a GRM, finding heritabilities that ranged from 0.1 for 'independence' in both German Shepherds and Labrador retrievers to 0.53 for 'tolerance to dogs' in Labrador retrievers and 0.82 for 'boldness' in German shepherds, with markedly different estimates in the two breeds [76]. In addition to sampling and genotyping differences (Friedrich *et al.* used array-based genotyping and 78 088 SNPs), within-breed heritabilities are expected to be variable across breeds owing to differences in both phenotypic and genotypic variation, especially given high rates of inbreeding in some breeds [78]. Given the range of heritabilities that we find in the current study, in addition to the variation observed across studies [75], it is likely that the approach to phenotyping (e.g. experimental versus observational) and specific methodological nuances also affect heritability estimates, as has been previously proposed [76]. It is also worth noting that our heritability estimates at the puppy timepoint may be inflated by the relative homogeneity of the puppies' experiences and environments.

The heritabilities we report here in the Canine Companions population are also smaller in general than those observed in humans [8]. There are many potential reasons for this, ranging from methodological to biological. Most human studies of heritability use twin studies, as opposed to relatedness matrices in a broader population. Nevertheless, genomic-relatedness (SNP-based) heritability is increasingly estimated for some traits; these studies tend to result in somewhat smaller heritability estimates, dependent in part on the SNP filtering criteria and sample size, owing to the large effects of rare variants, as well as population stratification [5,79–82]. The Canine Companions population consists of only two breeds and their crosses, is relatively inbred, and has been bred selectively for multiple decades, which might have caused reductions in both phenotypic and genotypic variation; heritabilities of certain traits might thus be higher in other breeds or populations of dogs (e.g. [76]). Furthermore, the Canine Companions population is managed such that individuals from a single litter are reared apart—from each other and their parents—after the first two months of life, perhaps disentangling genetic and environmental effects more completely than is possible or ethical in human studies, especially given indirect genetic effects induced by social stratification in human populations [19]. Many studies may also have focused specifically on traits that demonstrated high heritabilities, while potentially neglecting equally interesting cognitive and behavioural traits that are more malleable. Species differences could also be important, but they will be difficult to interpret until there are a wide variety of tasks studied across a large number of species [83].

We previously reported heritabilities for human-oriented social traits in puppies based on a subset of individuals included in this study [50], where we found moderately high heritability estimates for human interest looking times and point-following, with 43% of the task variation explained by pedigree-based relatedness for both tasks. In this larger sample, these estimates have decreased somewhat (within the credible intervals reported in [50]), but are still among the more heritable tasks at the puppy timepoint (human interest looking time h^2 = 0.32; pointing h^2 = 0.26). With the addition of longitudinal data, we now see changes in heritabilities from early life to adulthood, with the heritability of most traits staying relatively stable or decreasing across development. This is in contrast to longitudinal studies in humans that have found increased heritability of both verbal and nonverbal IQ over development in children [43]. A distinction between cognitive abilities and temperament or personality has been made in the human literature, with cognitive abilities tending to increase in heritability over time and personality traits decreasing in heritability over the lifespan [41]. We do not see this clear-cut distinction in dogs; however, we do see that the two temperament tasks—novel object and surprising events—display the largest decreases in heritability across development, despite being among the most heritable traits at both timepoints.

The observed decreases in the heritabilities of most of the DCDB measures can be interpreted in multiple ways that are not mutually exclusive. First, it is possible that genetic contributions to these traits decay during development and that environment, experience, learning and memory become more important determinants of phenotypic variation. Relatedly, in the Canine Companions population, individuals are raised apart after the puppy timepoint; thus, the general pattern of decreasing heritability could reflect the importance of environmental effects at any point in time, but the environments become more dissimilar after the two month timepoint. Reduced environmental variability tends to increase heritability estimates, as a larger fraction of the total phenotypic variance (the sum of genetic and environmental effects) becomes attributable to the genetic component. Thus, the relatively homogenous early environment in the current study may have contributed to the higher heritability estimates at this timepoint. Second, our sampling design makes it difficult to disentangle additive genetic effects from maternal or litter effects, and it is possible that the influence of these shared environmental effects wanes over time, as seen in humans [39]. Third, stochastic noise in measurement can artificially dampen heritability estimates; however, it is not clear why this effect would be larger for adults than puppies, given the high similarity between the testing procedures at each timepoint. Additionally, three measures—retrieval, unsolvable and cylinder detour—were estimated to be slightly more heritable in young adulthood, which is counter to the hypothesis that all adult phenotypes were characterized by greater stochastic variation. Thus, although our study provides evidence for reduced heritability of certain phenotypes at older ages, we cannot currently determine the cause of this phenomenon.

Our factor analyses indicate that there is surprisingly little correlation between any of the cognitive and behavioural traits measured by the DCDB and that these traits vary mostly independently from one another. This may be in part because we explicitly designed the battery to include tasks that were relatively unrelated and not redundant, as we intended to measure diverse aspects of dog behaviour and cognition in a reasonably concise battery. Nevertheless, the degree of independence among measured traits was unintended and contrasts with multiple previous studies, including some of our own work. Using a similar battery of tasks, MacLean *et al.* found evidence for six factors that clustered social and physical tasks separately, a pattern more similar to human children than to chimpanzees [84]. Using citizen science data from *Dognition.com*, Gnanadesikan *et al.* observed a four-factor structure, with factors for inhibitory control (although not the cylinder task), cooperative communication (including multiple pointing gestures), memory and physical reasoning [47]. In the present study, however, we did not find any evidence for a social cognition factor, executive function or any other latent cognitive trait that combined measurements across tasks. Our results also contrast with one report of a general intelligence factor in dogs based on three tasks (detour, point-following, quantity discrimination) [85], and another based on five tasks (persistence, one-trial learning, problem-solving success, associative learning and spatial working memory) [86]. The number and composition of tasks in the DCDB probably contributed to our lack of correlational structure [87,88]; this contrasts with batteries and surveys used in human studies that use multiple tasks or questions with only slight variations to measure a single theoretical construct such as spatial learning and memory [28,89] or personality [90]. The development and implementation of additional tasks and test batteries, as well as analyses that interrogate the importance of task selection may be informative in this regard. Another potential explanation for this discordant result is that the present study was conducted in a more homogeneous population than many previous studies that included individuals from multiple populations and breeds [47,84,86], and population-level confounds may produce spurious correlational structure. The relative standardization within the Canine Companions programme and our implementation of the cognitive testing may also have minimized pervasive confounding factors that would be more variable in other study populations, such as motivation owing to diet and feeding schedule, comfort in the testing arena, arousal owing to transportation and social interaction, visual and acoustic distraction, and other context effects. Further targeted work could assess the role of such factors on different phenotypes and inform methodological best practices. Given the independence of the measured phenotypes in our dataset, it is not surprising that the estimated heritabilities varied widely across traits. This also suggests that each phenotype may have substantially different underlying genetic bases and architecture.

We have not assessed the content or construct validity of the DCDB tasks reported here. For example, the social interpretation of several of these phenotypes has been questioned [91], and inhibitory control has repeatedly been shown to be context-dependent rather than a unitary construct [54,88,92–94]. We acknowledge that more work is needed in this regard. While some tasks were chosen based on a considerable volume of previous work in dogs and other species, other tasks—such as the 'human interest' task—were designed for this battery to measure a behaviour of interest in working dogs, and all tasks were refined for implementation with young puppies and in the context of this battery [48]. Because of the demands of such an extensive array of tasks, it was not possible to implement all of the controls necessary to rule out alternative explanations, although such efforts would be informative [88,95]. Nevertheless, we believe this large battery approach is fruitful for studying individual differences, which have long been understudied [85,88]. It is possible that issues of validity and repeatability could have affected our lack of observed factor structure and low heritability estimates for some traits. However, given the moderate-to-high heritabilities observed for other traits—as well as the biological relevance indicated by other association analyses, including the hormones oxytocin and cortisol [96]—we argue that the existing methods allow for the quantification of a variety of interesting, biologically meaningful phenotypes. We anticipate future work on these and other cognitive tasks will clarify their interpretation and validity, as well as the best methods for phenotyping traits of interest [88,97,98]. Cross-species comparisons may also shed light on the interpretation of specific cognitive tasks [99].

Dogs have become a preferred model for studying the biology underlying a variety of traits, including multiple aspects of behaviour. Our results suggest that additive genetic factors explain considerable variation in many cognitive and behavioural phenotypes in dogs, setting the stage for future work aimed at identifying molecular associations with these traits. Specifically, studies of more heritable traits will be most likely to detect significant associations and will require fewer individuals to be statistically well powered [100]. These estimates can also inform working dog organizations and other breeders in deciding which traits to attempt to affect through breeding versus through training, although heritabilities may be population-specific. Traits that are less heritable but are predictive of working dog success may be particularly suitable for training interventions in such populations [101]. More highly heritable traits will be more available to selection, although unintended consequences may arise and should be monitored, and the trade-offs inherent in such decisions may play out differently in dogs bred for different purposes [102].

5. Conclusions

Understanding the evolution of cognition is a challenging but important endeavour. As heritable variation is critical for evolution, studies of the genetic bases of behavioural and cognitive traits in diverse species are crucial. Our findings in dogs provide important data regarding both the structure of individual differences and the magnitude of potential genetic contributions to this variation. We found weak correlations among the phenotypic measures in this study, suggesting that selection could act relatively independently on these phenotypes, perhaps leading to domain-specific cognitive or behavioural adaptations. We also observed heritable variation for many traits, although the variance explained by additive genetic factors varied widely across phenotypes, indicating that some traits would respond more strongly to selective pressure than others. These heritability estimates were relatively robust to different methods of calculating relatedness amongst individuals but changed over development in some cases. In contrast to studies in humans, we find that measures of temperament are among the most heritable traits, although their heritability does decrease over time. The current work sets the stage for future studies designed to identify molecular associations with individual differences and emphasizes the importance of both development itself and changes in how genetic and environmental influences combine over the lifespan to shape phenotypic variation.

Ethics. Blood draws and behavioural testing procedures were approved by both Canine Companions and the University of Arizona Institutional Animal Care and Use Committee (IACUC no. 16-175) and were collected in accordance with relevant guidelines and regulations.

Data accessibility. Data and relevant code for this research work are stored in GitHub [103] and have been archived within the Zenodo repository [104]. Supplementary material is available online [105].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. G.E.G.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, visualization, writing—original draft, writing—review and editing; E.E.B.: conceptualization, data curation, funding acquisition, investigation, methodology, project administration, writing—review and editing; K.M.L.: investigation, methodology, writing—review and editing; D.J.H.: investigation, methodology, writing—review and editing; S.H.: investigation, writing—review and editing; L.E.L.C.D.: investigation, writing—review and editing; B.S.K.: investigation, project administration, resources, writing—review and editing; M.M.W.: methodology, writing—review and editing; N.S.-M.: methodology, resources, writing—review and editing; E.L.M.: conceptualization, funding acquisition, methodology, project administration, resources, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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