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Genetic parameters of personality traits in dogs based on behavioral assessment and questionnaire information

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ABSTRACT

A new behavior and personality assessment in dogs (BPH) was created in Sweden in 2012. Since the start of BPH, questionnaire data based on an extended version of C-BARQ have been collected to describe the everyday behavior of dogs. Our aim was to estimate genetic parameters for personality traits based on BPH or questionnaire data for eight breeds: American Staffordshire Terrier, Golden Retriever, Labrador Retriever, Lagotto Romagnolo, Nova Scotia Duck Tolling Retriever, Perro de Agua Español, Rhodesian Ridgeback, and Staffordshire Bullterrier. The number of BPH records ranged from 862 for Lagotto Romagnolo to 2462 for Labrador Retriever. Average heritability across all breeds was 0.22 for Sociability, 0.23 for Playfulness, 0.16 for Non-social fearfulness, 0.26 for Aggressiveness, and 0.22 for Boldness; all traits defined based on BPH. The genetic variation between breeds was larger than the genetic variation within breeds for Sociability, Playfulness, and Boldness. Estimates of heritability for questionnaire traits were more variable, possibly owing to fewer observations, and averages ranged from 0.06 to 0.28. Genetic correlations between BPH traits, on the one hand, and corresponding questionnaire traits, on the other hand, were consistently strong between Sociability and Stranger-directed interest (average 0.93) and Stranger-directed fear (-0.89); between Playfulness and Human-directed play interest (0.77); between Non-social fearfulness and Non-social fear (0.77); between Aggressiveness and Stranger-directed aggression (0.57); and between Boldness and Stranger-directed interest (0.78) and Stranger-directed fear (-0.80). Often, we could also see that a measure at BPH involving human interactions also extended to measure reactions to interactions with other dogs, e.g., a strong genetic correlation between Sociability and Dog-directed interest (0.58). In summary, selecting dogs based on traits defined at BPH is expected to result in behavioral changes not only when measured at BPH but also changes in everyday behavior in an expected way.

1. Introduction

Companion dogs often live closely alongside their owners and frequently encounter scenarios that can induce stress and fear, such as being exposed to sudden noises, heavy traffic, or unfamiliar objects, dogs and humans, or left alone at home (Sherman and Mills, 2008; Norling and Keeling, 2010; Stellato et al., 2017; PAW, 2024). A survey conducted by King et al. (2009) asked respondents to define their ideal companion dog, with results indicating a preference for dogs that are safe around children, friendly towards people (social), calm, and well-behaved. Research has found that behavioral issues are a leading cause of dogs being surrendered to shelters; common problems include hyperactivity, noisiness, and fearfulness (Wells and Hepper, 2000; Weng et al., 2006; Khoshnegah et al., 2011). Additionally, aggressive behavior is prevalent among dogs (Col et al., 2016) and can lead to severe consequences, such as biting incidents. Aggressive behavior may result in the dog being surrendered or even euthanized (Salman et al., 1998).

Stable individual differences in behavior in dogs, referred to as personality, have been found for several traits, such as fearfulness, sociability, and aggression (e.g., Jones and Gosling, 2005; Fratkin et al., 2013). This indicates that the risk of developing problematic behavior differs between individuals. Behavioral differences are not only seen between individual dogs within a breed but also among different breeds (Duffy et al., 2008; Hsu and Sun, 2010; Tiira et al., 2016; Salonen et al., 2020). Some breeds believed to exhibit dangerous behavior are subject to bans or restrictions in certain countries (Creedon & Ó Súilleabháin, 2017; Nilson et al., 2018; Anonymous, 2024). One solution for breeds with too high a proportion of dogs with behavioral issues is to breed for less problematic behavior. However, to perform genetic selection, we need to measure behavior consistently and reproducibly, ascertain

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sufficient genetic variation for the trait(s), and ensure that the measured trait(s) also predict everyday behavior.

In Sweden, two behavioral assessments for dogs have been developed. The Dog Mentality Assessment (DMA) is conducted by the Swedish Working Dog Association. Although initially designed for working breeds, the DMA gained popularity among owners and breeders of other breeds. Due to limited access to DMA for non-working breeds and a demand for a more general assessment from breeders and breed organizations, the Swedish Kennel Club (SKK) formed a development group to create a new assessment tool, primarily for behavioral-based dog breeding and the Behavior and Personality Assessment in Dogs (BPH in Swedish) was introduced in 2012 (Arvelius et al., 2012). Many subtests in the BPH are similar to those in the DMA, but modifications were made to accommodate dogs of different sizes, such as providing play objects of various sizes and a low-placed dummy for better visibility in the visual appearance subtest. Additionally, standardization was increased by using automated equipment and providing a more detailed procedural description. A substantial difference between the two assessments is that the BPH involves 241 potential behavioral ratings compared to the 33 ratings in the DMA.

Because DMA has been used in its current form since 1997, substantial work has been done to validate it. Studies based on DMA data suggest that the assessment identifies five or six specific traits, and a higher-order trait called Boldness. These traits remain consistent in rank order over repeated assessments about one month apart (Svartberg and Forkman, 2002; Svartberg et al., 2005). The validity of these traits has been supported by correlations with owner assessments and working dog trials, indicating their potential as indicators of working dog suitability and predictors of everyday behaviors, such as reactions to unfamiliar people and non-social fear (Svartberg, 2002, 2005). The traits have a genetic basis (Strandberg et al., 2005; Saetre et al., 2006; Arvelius et al., 2014) and have been used to develop estimated breeding values (EBVs) aimed at reducing fearfulness in dogs (Arvelius and Grandinson, 2012).

Owing to the shorter history of BPH, fewer studies have been done related to this assessment. A recent study used factor analysis to summarize behavioral ratings into broader factors and validated these phenotypically against everyday behavior defined from an owner questionnaire (Svartberg, 2021). To validate that traits defined from BPH can be used as selection tools to improve everyday behavior, it is necessary to evaluate the degree of genetic variation in the traits and their genetic correlation with everyday behavior traits. In a recent study, genetic analyses of BPH traits in eight breeds indicated low to intermediate heritability, suggesting genetic influences on these traits (Tygesen et al., 2025). Here, using a larger sample size, we estimated heritability for the traits identified in Svartberg (2021). Furthermore, we estimated genetic correlations among BPH traits as well as between BPH traits and behavioral subscales from a questionnaire. In addition, both within- and between-breed variation in behavior was analyzed.

2. Material and methods

2.1. Behavior and personality assessment in dogs (BPH)

The BPH is open to all dogs 12 months or older registered in the SKK and owned by a Swedish citizen. The BPH includes eight subtests: Unfamiliar person (S1), Object play (S2), Food interest (S3), Visual surprise (S4), Metallic noise (S5), Approaching person (S6), Unstable surface (S7) and Gunshots (S8, optional) (for details, see Table 1 in Svartberg, 2021). Each subtest has one to three phases, divided into sequences, as described in Svartberg (2021). The assessment, which takes approximately 45 minutes to complete, including a verbal summary, is carried out in a flat, open area of approximately 100 square meters, situated to limit disturbance. The equipment used in the BPH is developed or compiled centrally by the SKK and authorized organizers can purchase equipment from the SKK. The subtests are carried out in the same order

Table 1
Behavioral subscale scores (BSS) from the questionnaire, number of questions included in each BSS, and type of questions included in each BSS.

Behavior subscale score (acronym)	No. of questions	Questions describe the dog's…
Dog-directed interest (DDI)[a]	5	…eagerness to greet, approach, and play with unfamiliar dogs.
Stranger-directed interest (SDI)[a]	5	…willingness and eagerness to greet and approach unfamiliar persons.
Human-directed play interest (HDPI)[a]	5	…eagerness to play with an object (e.g., a ball, stick) together with familiar and unfamiliar humans.
Trainability (TRAIN)[b]	8	…willingness to pay attention to and obey the owner, and its ability to learn new tasks and to ignore distracting stimuli.
Dog-directed aggression (DDA)[b]	4	…dog's tendency to display aggressive reactions when approached by unfamiliar dogs.
Dog rivalry (DR)[c]	4	…aggressive behaviors towards other dogs in the household.
Stranger-directed aggression (SDA)[b]	10	…threatening or aggressive reaction towards unfamiliar persons approaching or invading the dog, the owner or the dog's or the owner's territory.
Owner-directed aggression (ODA)[b]	8	…threatening or aggressive behavior towards the owner or other household members when verbally corrected or punished, challenged, stepped over, during handling, or when approached while in possession of food or objects.
Dog-directed aggression or fear (DDAF)[b]	8	…tendency to display aggressive or fearful reactions when approached by unfamiliar dogs. Combination of DDA and DDF.
Dog-directed fear (DDF)[b]	4	…tendency to display fearful reactions when approached by unfamiliar dogs.
Stranger-directed fear (SDF)[b]	4	…the degree of fearful reactions when approached by unfamiliar persons.
Non-social fear (NSF)[b]	6	…tendency to show fearful or wary responses to sudden or loud noise, in heavy traffic, to unfamiliar situations and objects, during thunderstorms, and to wind or wind-blown objects.
Attachment and attention seeking (AAS)[b]	6	…propensity to stay close to the owner and to seek attention, and how agitated it becomes when the owner directs his/her attention towards someone else.
Separation-related behavior (SRB)[b]	8	…tendency to vocalize, shake, tremble, salivate, scratch at doors, etc., when left, or about to be left, alone.
Excitability (EX)[b]	6	…how strongly the dog reacts to potentially exciting or arousing events, e.g., going for a walk or a car ride or the doorbell signal.
Energy level (EL)[c]	2	…how energetic, active, and playful the dog is.
Chasing (CHASE)[b]	4	…tendency to chase after cats, birds, and other small animals (if given the opportunity).
Touch sensitivity (TS)[b]	4	…fearful or wary reaction to potentially painful situations, e.g., when being groomed, bathed, or examined by a veterinarian.
Situational fear (SF)[d]	10	…fearful reaction to unknown or unusual situations, e.g., walking on unsteady surfaces or slippery floors, when high above the ground or in tight spaces.
Social fear and aggression (SFA)[d]	6	… fearful or aggressive reaction when being surprised by an unknown person or dog or approached by a person that looks strange or moves in a strange way.
Fear recovery latency (FRL)[d]	5	… tendency to show flight or passive behavior when scared and take a long time to recover.
Stubborn and curious (SC)[d]	4	…curiosity when something unexpected happens and persistency in efforts to get something desirable.

[a] First described by Svartberg (2005)
[b] First described by Hsu and Serpell (2003)

[c] First described by Duffy and Serpell (Duffy and Serpell, 2012)
[d] Defined in this study

for each dog. Three individuals are involved in the assessment: an assessment leader, a rater, and a figurant, all trained and authorized by the SKK. The assessment leader is the handler's guide during the assessment (encountered first in S1, where the assessment leader acts as the unfamiliar person), the rater makes all behavioral assessments, and the figurant is acting in S6 (as the approaching person) and S8 (the shooter of the gunshots).

Svartberg (2021) used a hierarchical factor analysis procedure to identify behavioral traits in the BPH. At a four-factor level, Sociability, Playfulness, Non-social fearfulness, and Aggressiveness were identified and defined. These traits, together with a higher-order trait labelled Boldness, which appeared at the first factor level in Svartberg (2021), were used in this study. Sociability was created from greeting in S1 & S6 (positive weights, +) and fear-related variables in S1 and S6 (negative weights, using a reversed scale, -). Playfulness was created from play variables in S2 (+) and from disinterest in S2 (-). Non-social fearfulness was created from fear-related variables in S4, and S5, S6, and S7 (+), and from exploration in S4 and S5 (-). Aggressiveness was created mainly from threat and avoidance variables in S6 but also from threat variables in S4 (+). Finally, Boldness was created from greeting (S1 & S6), play variables (S2) and exploration (S4 & S5) (+), and from fear-related variables (S1, S4, S5, S6 & S7) (-).

2.2. Dog owner questionnaire

A web-based questionnaire was created to get information about the dogs' behavior in everyday life. It was open from September 2012 and for the current study, answers were retrieved in June 2023. The questionnaire was open to any dog owner, and a link to the questionnaire was posted on the SKK website. Owners participating in the BPH were encouraged to answer the questionnaire. The owners were requested to supply the dog's SKK registration number.

The questionnaire was based on the standardized Canine Behavioral Assessment and Research Questionnaire (C-BARQ), which was developed as a tool for the selection of guide dogs (Serpell and Hsu, 2001) but was later extended to make it possible for a dog owner to describe the dog's typical behavior (Hsu and Serpell, 2003). A Swedish translation was done and, together with some additional items, it was used to validate the Swedish Dog Mentality Assessment (DMA) (Svartberg, 2005). That battery of items, with some further added items to provide more information about specific behaviors, was used in the questionnaire in our study (Suppl. Table 1). The questionnaire consisted of 132 items for which the respondent used a five-grade scale to describe the dog's typical behavior in the recent past when exposed to certain stimuli. There were two scales used in the questionnaire; one indicated the severity of the behavior (how much of the behavior the dog showed) on a scale of 1 (no sign of the behavior) to 5 (severe form of the behavior) (71 questions); the other indicated how often the dog showed the behavior (the scale was never to always, 61 questions, also five levels (1−5). The items could be condensed into 18 behavior subscale scores (BSS) (Table 1) according to previous literature (Hsu and Serpell, 2003; Svartberg, 2005; Duffy et al., 2008). However, we decided to use the more general subscale Dog-directed aggression or fear (DDAF), but not its two component traits, Dog-directed aggression (DDA) and Dog-directed fear (DDF).

Some questions were not previously included in the factor analysis used to define the 18 BSS. Therefore, a factor analysis was done solely on these 31 questions to find additional BSS that could be of interest in relation to BPH. Polychoric correlations were used as input to Proc Factor in SAS (2016), using varimax rotation. This resulted in four factors with eigenvalues > 1, named Situational fear (SF), Social fear and aggression (SFA), Fear recovery latency (FRL), and Stubborn and curious (SC) (Table 1). Cronbach's alpha for these four BSS were 0.77, 0.78, 0.72, and 0.57, respectively. All BSS were defined as the average value of the included items, and missing values were ignored.

2.3. Subjects

The breeds studied were those with the most observations for BPH. Considering that we intended to also estimate genetic correlations, we decided not to go below 800 observations, which resulted in 8 breeds: American Staffordshire Terrier, Golden Retriever, Labrador Retriever, Lagotto Romagnolo, Nova Scotia Duck Tolling Retriever, Perro de Agua Español, Rhodesian Ridgeback, and Staffordshire Bull Terrier. Number of dogs with observations for BPH traits as of 2023–11–01 are shown in Table 2. If a dog had more than one BPH record, only the first was kept. In total, around 11,850 dogs were analyzed, out of which 45 % were males. Only 5.5 % of dogs were castrated (7.5 % of males and 3.8 % of females). Almost 70 % of the dogs were between 12 and 24 months of age, and another 20 % were between 24 and 36 months.

Number of dogs with observations for questionnaire traits is shown in Table 2. In total, 3962 dogs had information on questionnaire traits, 47 % being male dogs. For most traits, the number of observations was similar for a given breed; however, for Dog rivalry (DR), much fewer dogs had scores because it requires at least one more dog in the household. Fewer dogs had information on both BPH traits and questionnaire traits, 2672 (except for DR, 1667).

2.4. Statistical analysis

For the BPH traits, the fixed effects of sex, linear and quadratic regressions on age at assessment (from 12 months of age, dogs older than 48 mo. were set to 48 mo.) and assessment year, all nested within breed, were tested in a fixed linear model using the function lm in R (R Core Team, 2021). Based on the results, all three factors were included in the final model for all breeds and traits (the quadratic effect of age was not significant for Aggressiveness, but the term was still included). Various random effects were also tested with the three fixed factors and additive genetic effect of the individual dog in the model, using the Akaike Information Criterion (AIC) within the AIREML procedure in the software DMU (Madsen and Jensen, 2013). The factors tested were rater, assessment leader, arranging partner (breed club et cetera), dam, and litter. The first three factors attempt to catch influences on the actual assessment situation and were tested as single factors or combinations. Dam and litter are trying to catch influences that permanently affect the dog from birth. These two were tested as single factors and jointly. Finally, single factors or combinations of rater, assessment leader, and arranging partner were tested with single or combined effects of dam and litter. AIC-values were compared between models and with the

Table 2
Number of dogs with observations for various traits in the Behaviour and Personality Assessment (BPH) and in the questionnaire (all questions except dog rivalry (DR) and questions relating to dog rivalry).

		Questionnaire		Both BPH and questionnaire	
Breed[a]	BPH[2]	All except DR[2]	DR	All except DR[2]	DR
AST	878	286	198	153	96
GR	1535	839	548	372	240
LAB	2461	630	418	571	380
LAG	860	527	270	241	123
NSDTR	1497	516	355	373	270
PDAE	982	209	112	200	107
RR	1938	652	382	486	279
SBT	1699	303	193	276	172
Total	11,850	3962	2476	2672	1667

[a] AST = American Staffordshire Terrier; GR = Golden Retriever; LAB = Labrador Retriever; LAG = Lagotto Romagnolo; NSDTR = Nova Scotia Duck Tolling Retriever; PDAE = Perro de Agua Español; RR = Rhodesian Ridgeback; and SBT = Staffordshire Bull Terrier. [2] Average across traits.

model with additive genetic effect of the dog as the only random component. This was done for the smallest breed, Lagotto Romagnolo. The final model included rater and assessment leader:

$$y_{ijklmn} = \mu + sex_i + b_1\, age_j + b_2\, age_j^2 + year_k + r_l + al_m + a_n + e_{ijklmn} \quad (1)$$

where y_{iklmn} is the observation for the given BPH trait, μ is the overall mean, sex_i is the fixed effect of sex i (male, female), age_j and age_j^2 is the age and age squared at assessment, respectively, $year_k$ is the year of assessment (2012, 2013, …, 2023), r_l is the random effect of rater l, $\sim N(\mathbf{0}, \mathbf{I}\sigma_r^2)$, al_m is the random effect of assessment leader m, $\sim N(\mathbf{0}, \mathbf{I}\sigma_{al}^2)$, a_n is the random additive genetic effect of dog n, $\sim N(\mathbf{0}, \mathbf{A}\sigma_a^2)$, where $\mathbf{A}$ is the additive genetic relationship matrix, $\mathbf{I}$ is an identity matrix, and e_{ijklmn} is the residual, $\sim N(\mathbf{0}, \sigma_e^2)$. A bivariate version of the above model was used to estimate genetic correlations among BPH traits, however, without covariances for rater and assessment leader effects, to improve the convergence of the models. Because the BPH traits were averages of several scores, some of which could be missing for a given dog, a weighted analysis was carried out, using the proportion of available scores as weight for the residual variance.

Also for questionnaire traits, only dogs with a correct SKK registration number were considered. Pedigree information, sex, and birth date of the dog were available from SKK, and using the questionnaire answer date, the dog's age at the time the questionnaire was filled out was calculated. The model was:

$$y_{ijn} = \mu + sex_i + ageq_j + a_n + e_{ijn} \quad (2)$$

where y_{ijn} is the observation for the given questionnaire trait, μ is the overall mean, sex_i is the fixed effect of sex i (male, female), $ageq_j$ is the age of the dog at the time the questionnaire was filled out (age classes <15 mo, 15–17, 18–20, 21–23, 24–35, 36–46, 47-), a_n is the random additive genetic effect of dog n, $\sim N(\mathbf{0}, \mathbf{A}\sigma_a^2)$, and e_{ijn} is the residual, $\sim N(\mathbf{0}, \mathbf{I}\sigma_e^2)$. A bivariate analysis combining models [1] and [2] was used to estimate the genetic correlation between BPH traits and questionnaire traits, with the residual correlation set to zero (not estimated).

All estimates of genetic parameters were derived using the AIREML procedure in the software DMU (Madsen and Jensen, 2013). Regardless of trait or model, heritability was always defined as $\sigma_a^2/(\sigma_a^2 + \sigma_e^2)$. For BPH traits, the variance ratios for the rater and the assessment leader

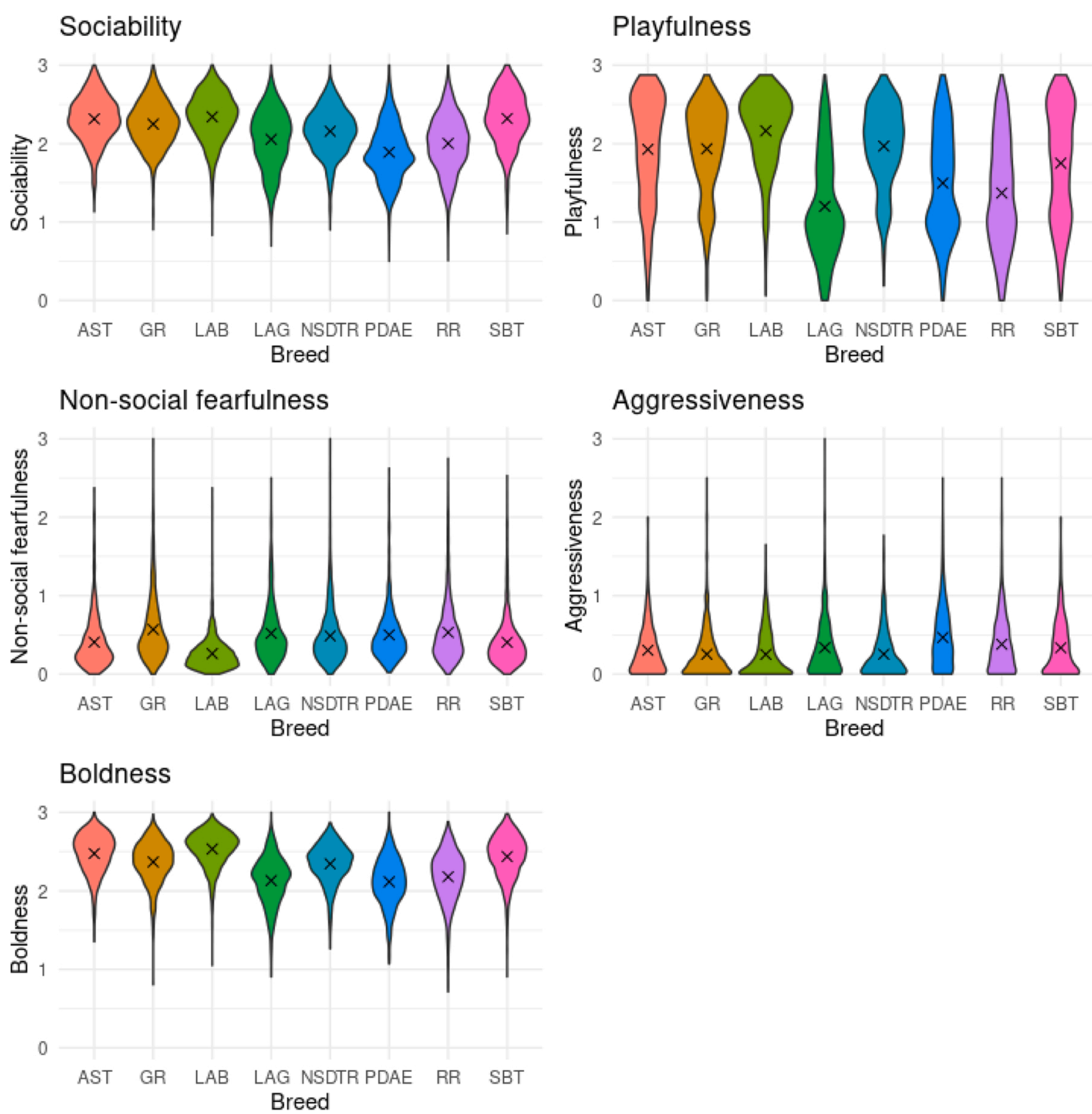

Fig. 1. Violin plot of averages and variability for BPH traits for eight breeds (AST = American Staffordshire Terrier; GR = Golden Retriever; LAB = Labrador Retriever; LAG = Lagotto Romagnolo; NSDTR = Nova Scotia Duck Tolling Retriever; PDAE = Perro de Agua Español; RR = Rhodesian Ridgeback; and SBT = Staffordshire Bull Terrier). The X indicates the average value.

were calculated as $\sigma_r^2/(\sigma_a^2+\sigma_r^2+\sigma_{al}^2+\sigma_e^2)$ and $\sigma_{al}^2/(\sigma_a^2+\sigma_r^2+\sigma_{al}^2+\sigma_e^2)$, respectively.

To study the variation among the eight breeds for BPH and questionnaire traits, a linear model with only an overall mean and a random effect of breed was used with the lmer function in R (R Core Team, 2021), and a ratio of between-breed variance versus total variance was calculated for each trait. The average within-breed heritability was also expressed on this scale, to compare the proportion of between-breed and within-breed genetic variation. For this calculation, the within-breed heritability included all four variance components in the denominator. As an example, if the between-breed variation was 20 % of total variation and heritability was 25 %, the within-breed genetic variance proportion was 0.25 * 0.8 = 0.2, in this case indicating that the between and within-breed variation was of similar size.

3. Results

3.1. Descriptive statistics of breed averages and within-breed variation

Averages and variability for BPH traits are shown in Fig. 1, and for some questionnaire traits in Fig. 2. Standard errors of means for BPH traits ranged from 0.005 to 0.02. Labrador Retriever, American

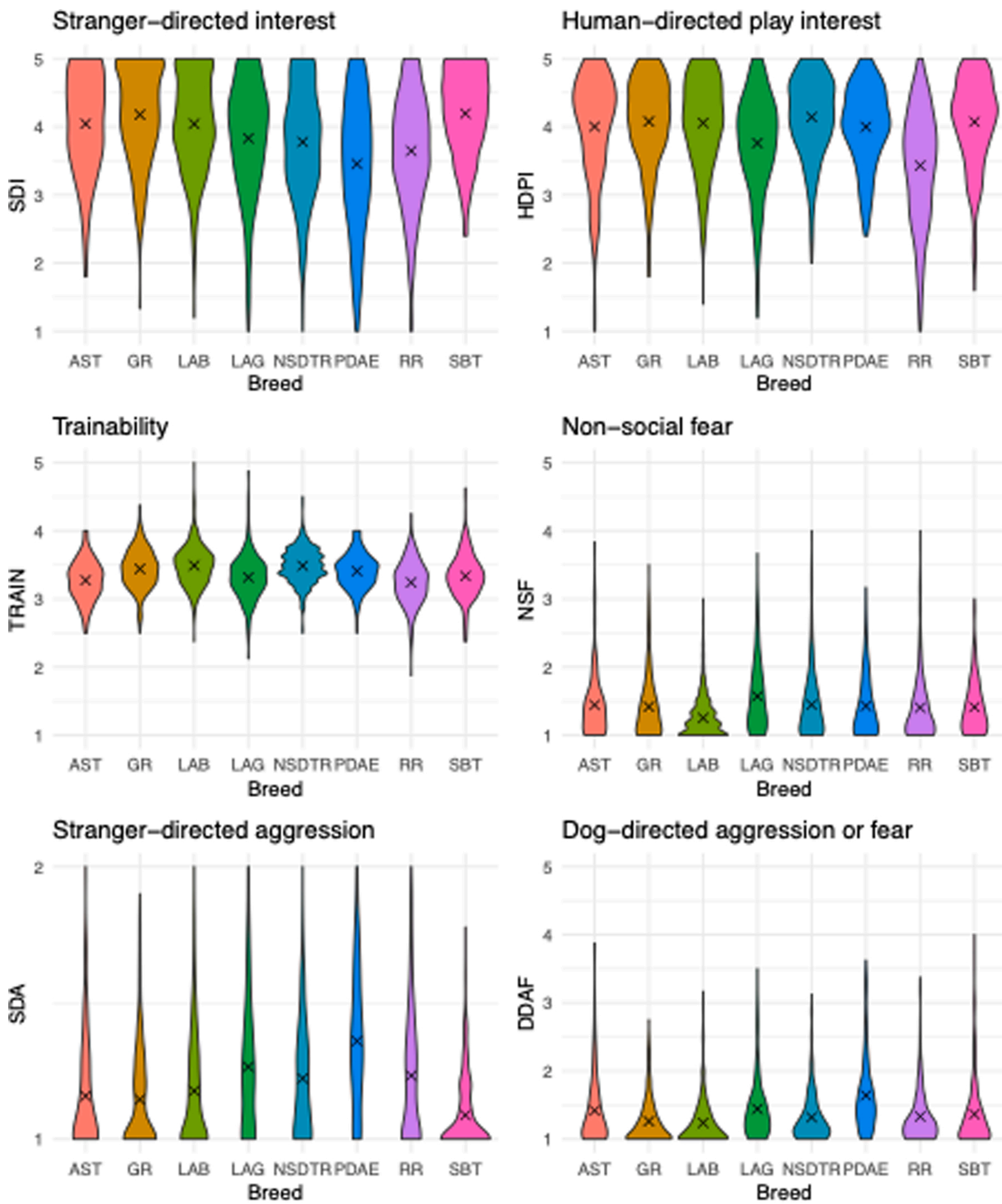

Fig. 2. Violin plot of averages and variability for some questionnaire traits for eight breeds (AST = American Staffordshire Terrier; GR = Golden Retriever; LAB = Labrador Retriever; LAG = Lagotto Romagnolo; NSDTR = Nova Scotia Duck Tolling Retriever; PDAE = Perro de Agua Español; RR = Rhodesian Ridgeback; and SBT = Staffordshire Bull Terrier). The X indicates the average value. Note that the scale for SDA has been cut to improve visibility.

Staffordshire Terrier, and Staffordshire Bull Terrier had the highest average for Sociability and Boldness. Labrador Retriever also had the highest Playfulness and the lowest Non-social fearfulness and Aggressiveness (the latter together with Golden Retriever and Nova Scotia Duck Tolling Retriever). Lagotto Romagnolo had the lowest average Playfulness; Perro de Agua Español had the lowest Sociability and Boldness and the highest Aggressiveness. Golden Retriever had the highest average Non-social fearfulness.

For some of the breeds, a similar pattern was seen for the questionnaire traits. Labrador Retriever had high or highest values for Dog-directed interest, Stranger-directed interest, Human-directed play interest, and Trainability, but also low or lowest values for fear- and aggression-related traits (Dog rivalry, Stranger-directed aggression, Owner-directed aggression, Dog-directed aggression or fear, Non-social fear, Social fear and aggression, and Fear recovery latency). On the other hand, Perro de Agua Español had high or highest values for the same fear- and aggression-related traits.

Although the averages can differ significantly, e.g., for Playfulness between Labrador Retriever and Lagotto Romagnolo, there was substantial variation within breeds for all traits and subscales. In all cases, there was considerable overlap of distributions, e.g., a sizeable proportion of Lagotto Romagnolo (11 %) was more playful than the average Labrador Retriever. This considerable phenotypic variation within breeds is a prerequisite for the existence of genetic variation.

3.2. Test of fixed factors in the models

For BPH traits, sex differences were found in 73 % of breed by trait combinations with $P < 0.05$. Generally, females showed less Playfulness (on average −0.18 units), slightly lower Sociability (-0.04) and Boldness (-0.08), and marginally higher Non-social fearfulness (+0.05). P-values for the year of assessment were < 0.05 in 75 % of breed by trait combinations. One should remember that in this simple model, there is no account taken of any genetic change in the traits. For age at assessment as linear and quadratic regression, either or both p-values were < 0.05 in 58 % of all combinations of breed and trait. For the breed by trait combinations where age had a significant effect ($P < 0.05$), the general tendency was a decrease in value for all five BPH traits. However, the only substantial decrease was found for Playfulness in Rhodesian Ridgeback, with a reduction of about 0.8 units from 12 to 48 months of age (Suppl. Figure 1).

For questionnaire traits, sex and age were only significant ($P < 0.05$) in 24 % and 32 % of all combinations of breed and trait, respectively. Females had lower values for Dog-directed interest, Human-directed play interest, Trainability, Owner-directed aggression, Separation-related behavior, Excitability, and Energy level but higher values for Dog rivalry, Stranger-directed aggression, Stranger-directed fear, Chasing, and Social fear and aggression. For other traits, the sex differences were small. Dog-directed interest, Stranger-directed interest, Human-directed play interest, Energy level, and Stubborn and curious all decreased with age, whereas Dog-directed aggression or fear tended to increase slightly with age (Suppl. Figure 2). Other traits showed less clear trends (results not shown).

3.3. Test of random factors in the models for BPH traits

For random effects, tested for Lagotto Romagnolo, in general, no model was universally best, however, dam and/or litter were hardly ever included among the top-ranked models. Rater, assessment leader, and/or arranging partner and their combinations were among the top-rated models (+5 units of AIC). However, one or several of the included variance components were often not significantly different from zero even if a model had the best AIC. We decided to include both rater and assessment leader even though one of them might have sufficed, and exclude arranging partner, also because it had fewer levels. Regardless of what random factors were included, heritability estimates were very robust.

3.4. Estimates of heritability and variance ratios

Heritability estimates for BPH traits are shown in Table 3. The average of heritability estimates across breeds for BPH traits was rather similar, 0.16–0.26 but the range of individual estimates was quite large, from 0.07 to 0.38. Average SE(h^2) across breeds ranged from 0.048 to 0.061 (not shown).

For questionnaire traits, heritability estimates varied more widely (Table 4 and Suppl. Table 2). For some breeds, several estimates were zero, especially for Perro de Agua Español. Also, some traits were more likely to have very low heritability, e.g., Trainability, Dog rivalry, and Owner-directed aggression. Dog rivalry had fewer observations than the other traits (Table 2), and Owner-directed aggression was uncommon. These issues notwithstanding, several traits had consistently non-zero estimates and average heritabilities were estimated between 0.14 and 0.28. Overall, average heritability was 0.17. Owing to the fewer observations, the SEs were also higher than for BPH traits, averaging from 0.08 to 0.17 for various breeds (Suppl. Table 2).

Variance ratios for rater were highest for Sociability and Aggressiveness (10 % and 8 %, respectively) but otherwise low (2–4 %). For individual breeds, the variance ratio ranged from 7 % to 15 % for Sociability (Perro de Agua Español and Golden Retriever, respectively) and from 2 % to 17 % (American Staffordshire Terrier and Perro de Agua Español, respectively) (not shown). Variance ratios for assessment leader were low, around 3 %.

3.5. Estimates of genetic correlation

Estimates of genetic correlation among BPH traits are shown in Suppl. Table 3 and averages across breeds in Table 3. The genetic correlation between Sociability and Playfulness was generally positive, with an average of 0.31. The average genetic correlation between Sociability, on the one hand, and Non-social fearfulness or Aggressiveness, on the other hand, was of similar size but was negative (−0.24 and −0.28, respectively). The average genetic correlation between Playfulness, on the one hand, and Non-social fearfulness or Aggressiveness, on the other hand, was −0.19 and −0.11, and the correlation between Non-social fearfulness and Aggressiveness was of similar size but was positive. Boldness was strongly positively correlated with Sociability (0.77) and Playfulness (0.64) and negatively correlated with Non-social fearfulness (−0.57) and Aggressiveness (-0.28). In summary, genetically more bold, social, and playful dogs are less non-socially fearful and aggressive, and more fearful dogs are also genetically slightly more aggressive.

Average estimates of genetic correlation between BPH traits and questionnaire traits are shown for five breeds in Table 5. For three of the breeds (American Staffordshire Terrier, Perro de Agua Español, and Staffordshire Bull Terrier), the SEs of the heritability estimates for the questionnaire traits were, on average, so high (0.14–0.17) that it was decided not to attempt to estimate genetic correlations. Also, the genetic correlation involving a questionnaire trait with zero heritability for a given breed was not estimated. In general, estimates were variable between breeds and had large SE with the bulk of SE spread around 0.2 but with a long right tail (not shown). Nevertheless, many correlation estimates were consistently positive or negative across breeds, shown in blue or red in Table 5, and sometimes very strong. Sociability and Boldness had similar correlation patterns, with high and consistently positive genetic correlations with Dog-directed interest and Stranger-directed interest and strong and consistently negative correlations with Stranger-directed aggression, Stranger-directed fear, and Social fear and aggression. Playfulness was consistently strongly positively genetically correlated with especially Human-directed play interest. Fewer strong correlations were obtained for the remaining BPH traits. However, Non-social fearfulness had high correlations with Non-social

Table 3
Heritability estimates (± SE) for the BPH traits Sociability, Playfulness, Non-social fearfulness, Aggressiveness, and Boldness for eight breeds and average (± SD) across eight breeds; average variance ratios for rater (VR_r) and assessment leader (VR_{al}) (± SD); average genetic correlations (± average SE) across eight breeds.

Breed[a], item or trait	Trait Sociability	Playfulness	Non-social fearfulness	Aggressiveness	Boldness
AST	0.13 ± 0.06	0.13 ± 0.06	0.21 ± 0.07	0.27 ± 0.08	0.13 ± 0.06
GR	0.15 ± 0.06	0.29 ± 0.06	0.20 ± 0.05	0.14 ± 0.06	0.19 ± 0.05
LAB	0.28 ± 0.05	0.18 ± 0.05	0.24 ± 0.05	0.22 ± 0.05	0.29 ± 0.05
LAG	0.15 ± 0.07	0.23 ± 0.07	0.12 ± 0.06	0.24 ± 0.08	0.12 ± 0.06
NSDTR	0.19 ± 0.05	0.26 ± 0.06	0.18 ± 0.05	0.25 ± 0.06	0.21 ± 0.06
PDAE	0.22 ± 0.07	0.15 ± 0.05	0.07 ± 0.04	0.25 ± 0.08	0.20 ± 0.06
RR	0.31 ± 0.05	0.27 ± 0.05	0.22 ± 0.04	0.37 ± 0.06	0.38 ± 0.05
SBT	0.23 ± 0.05	0.23 ± 0.05	0.07 ± 0.04	0.32 ± 0.06	0.24 ± 0.05
Ave. ± SD	0.21 ± 0.06	0.22 ± 0.06	0.16 ± 0.07	0.26 ± 0.07	0.22 ± 0.09
VR_r ± SD	0.10 ± 0.03	0.02 ± 0.01	0.02 ± 0.01	0.08 ± 0.05	0.04 ± 0.01
VR_{al} ± SD	0.03 ± 0.02	0.02 ± 0.02	0.03 ± 0.02	0.03 ± 0.02	0.03 ± 0.02
Average genetic correlations (± average SE)					
Sociability		0.31 ± 0.19	−0.24 ± 0.22	−0.28 ± 0.20	0.77 ± 0.09
Playfulness			−0.19 ± 0.21	−0.11 ± 0.20	0.64 ± 0.13
Non-social fearfulness				0.16 ± 0.22	−0.57 ± 0.16
Aggressiveness					−0.28 ± 0.20

[a] AST = American Staffordshire Terrier; GR = Golden Retriever; LAB = Labrador Retriever; LAG = Lagotto Romagnolo; NSDTR = Nova Scotia Duck Tolling Retriever; PDAE = Perro de Agua Español; RR = Rhodesian Ridgeback; and SBT = Staffordshire Bull Terrier.

Table 4
Average heritability estimates for the questionnaire traits for eight breeds.

Trait	Average heritability
Dog-directed interest (DDI)	0.28
Stranger-directed interest (SDI)	0.22
Human-directed play interest (HDPI)	0.28
Trainability (TRAIN)	0.12
Dog rivalry (DR)	0.10
Stranger-directed aggression (SDA)	0.22
Owner-directed aggression (ODA)	0.06
Dog-directed aggression or fear (DDAF)	0.22
Stranger-directed fear (SDF)	0.26
Non-social fear (NSF)	0.19
Attachment and attention seeking (AAS)	0.12
Separation-related behavior (SRB)	0.19
Excitability (EX)	0.11
Energy level (EL)	0.20
Chasing (CHASE)	0.17
Touch sensitivity (TS)	0.17
Situational fear (SF)	0.14
Social fear and aggression (SFA)	0.14
Fear recovery latency (FRL)	0.09
Stubborn and curious (SC)	0.15

fear, Situational fear, and Fear recovery latency. The correlations with Aggressiveness were in general lower, with the highest correlation with Stranger-directed aggression of 0.57.

3.6. Estimates of between and within-breed variation

The relation of between-breed to within-breed genetic and non-genetic variation is shown in Fig. 3. For Sociability, Playfulness, and Boldness, the between-breed variation was larger (22–26 %) than the within-breed genetic variation (14–16 %), whereas for Non-social fearfulness and Aggressiveness, the between-breed variation was quite small (5–8 %). For questionnaire traits, the average between-breed variation proportion was only 6 %, whereas the within-breed genetic proportion was 17 %.

4. Discussion

We found genetic variation for BPH traits both between and within breeds, with heritabilities around 0.2. We also found a genetic variation of similar size for questionnaire traits, however, with larger variability and lower precision. Most importantly, we found strong genetic correlations between BPH and questionnaire traits that measure similar kinds of behavior. This indicates that BPH can be used as a selection tool to change everyday behavior within dog breeds.

4.1. Estimates of heritability and variance ratios

In a meta-analysis, Hradecká et al. (2015) found the average heritability for various behavioral traits to vary between 0.09 and 0.15. The heritability for BPH traits in our study was, on average, around 0.2, however, not without exceptions. For Non-social fearfulness, the heritability estimate was as low as 0.05–0.07 for Lagotto Romagnolo, Perro de Agua Español, and Staffordshire Bull Terrier. This means it would be more difficult for these breeds to achieve genetic change for this trait. On the other hand, the heritability was almost 0.4 for Aggressiveness in Rhodesian Ridgeback and around 0.3 for several trait-breed combinations. Overall, the heritability estimates indicate that selecting based on these BPH traits can be done with acceptable accuracy (correlation between the selection criterion and the true breeding value), on average about 0.45 (square root of heritability). However, with a genetic evaluation using mixed linear models (BLUP), the accuracy would be even higher, given the information from relatives. The heritabilities found here are within the range of heritabilities found for milk, fat, and protein production in dairy cattle (0.15–0.58), for which substantial genetic progress has been achieved (Miglior et al., 2017).

In general, our heritability estimates were in line with what Tygesen et al. (2025) found in a smaller sample of the same eight breeds. In particular, there were only small differences in the estimates for the two most similarly defined traits, Sociability and Playfulness (Sociality and Playful behavior in Tygesen et al., 2025), with average estimates of 0.21 vs 0.21 and 0.22 vs 0.19, respectively. This indicates that the differences in estimates to some degree may be due to differences in the definition of behavior traits. The most notable difference of 0.11 in averages was found for Non-social fearfulness (our study) and Flight and distancing behavior (Tygesen et al., 2025). These two traits are similar, but the trait scores are based on somewhat different behavior measures and calculated differently (we used representative values and actual protocol scores, whereas Tygesen et al., (2025) standardized the scores and calculated the factor scores using factor loadings as weights). Another difference was that the dogs in our sample were between 12 and 48 months old when carrying out BPH, whereas the oldest dog in Tygesen et al., (2025) was more than 12 years old.

Several traits in the BPH are equivalent or at least comparable to those found in the DMA (Svartberg, 2022). Overall, the heritability

Table 5
Average of genetic correlations between questionnaire traits and traits from behavioral assessment BPH for five breeds. The blue (red) color indicates that correlations were positive (negative) for all five breeds[a].

	BPH trait				
Questionnaire trait, acronym	Sociability	Playfulness	Non-social fearfulness	Aggressiveness	Boldness
Dog-directed interest, DDI	0.58	0.35	-0.16	-0.28	0.55
Stranger-directed interest, SDI	0.93	0.29	-0.06	-0.27	0.78
Human-directed play interest, HDPI	0.37	0.77	-0.12	0.02	0.55
Trainability, TRAIN	0.16	0.48	-0.28	-0.14	0.31
Dog rivalry,DR	-0.56	0.22	0.07	0.32	-0.13
Stranger-directed aggression, SDA	-0.65	-0.38	0.06	0.57	-0.62
Owner-directed aggression, ODA	-0.14	-0.17	-0.18	-0.14	-0.10
Dog-directed aggression or fear, DDAF	-0.55	-0.31	0.10	0.36	-0.58
Stranger-directed fear, SDF	-0.89	-0.47	0.25	0.47	-0.80
Non-social fear, NSF	-0.47	-0.27	0.77	0.22	-0.71
Attachment and attention seeking, AAS	-0.12	-0.11	-0.27	0.11	0.00
Separation related behavior, SRB	0.08	-0.21	-0.03	-0.02	-0.11
Excitability, EX	0.06	-0.08	-0.16	0.24	-0.07
Energy level, EL	0.51	0.52	-0.29	0.27	0.55
Chasing, CHASE	0.04	0.20	-0.03	0.35	0.06
Touch sensitivity, TS	-0.38	-0.10	0.36	0.21	-0.58
Situational fear, SF	-0.48	-0.19	0.88	0.50	-0.76
Social fear and aggression, SFA	-0.81	-0.45	0.38	0.51	-0.71
Fear recovery latency, FRL	-0.53	-0.22	0.80	0.06	-0.82
Stubborn and curious, SC	0.19	0.33	-0.44	0.17	0.53

[a] Golden Retriever, Labrador Retriever, Lagotto Romagnolo, Nova Scotia Duck Tolling Retriever, and Rhodesian Ridgeback.

estimates in our study are approximately within the same range as what has been found for comparable DMA traits. For example, Strandberg et al. (2005) and Arvelius et al. (2014) reported that in Germans Shepherd Dogs and Rough Collie the estimates for DMA Sociability, Playfulness, and Curiosity/fearlessness (equivalent to reversed BPH Non-social fearfulness) were similar or slightly higher, whereas the estimates for BPH Aggressiveness were about 0.10 lower on average. For Boldness, Strandberg et al. (2005) estimated a heritability of 0.27 in German Shepherd Dogs and Saetre et al. (2006) found a heritability of 0.25–0.27 in German Shepherd Dogs and Rottweilers, which could be compared to the estimates in our study ranging from 0.12 to 0.38. However, the breeds differ between these studies and ours, which makes more specific comparisons difficult. One exception is the study of Sundman et al. (2016) in which several traits based on DMA for Golden and Labrador Retrievers were defined. They found heritability estimates of 0.19–0.21 for Social greeting (similar to Sociability), 0.13–0.35 for Play interest, 0.30–0.32 for Curiosity (/fearlessness), and 0.28–0.39 for Threat display (similar to Aggressiveness). If we compare with the estimates in this study for Golden and Labrador Retrievers, our estimates for Sociability and Playfulness are slightly lower for Golden Retriever but slightly higher for Labrador Retriever (by about ± 0.04–0.07) than theirs. However, for Non-social fearfulness (Curiosity in Sundman et al. 2016) and Aggressiveness, our estimates were consistently lower, with up to 0.25 (Golden Retriever, Aggressiveness). It should be mentioned that their heritability estimate of 0.39 is much higher than in any other study. Also, even though the breeds (Golden Retriever, Labrador Retriever) are the same, their study was based on dogs described in DMA 2005–2014, whereas our study used dogs described in BPH 2012–2023.

For the questionnaire traits, heritability estimates varied more widely with some being zero, probably due to the smaller sample size than the BPH sample. The averages of the non-zero estimates were between 0.14 and 0.28. The highest heritability was found for Human-directed play interest, a subscale for which high estimates previously have been reported (Arvelius et al., 2014; Eken Asp et al., 2014). The lowest estimate was for Owner-directed aggression (0.06). This subscale is characterized by very low variation, i.e., only a few owners have noted this behavior. This may have caused the low heritability, which is in line with estimates from other studies (Arvelius et al., 2014; Eken Asp et al., 2014; Ilska et al., 2017). Overall, the heritability estimates are near what has previously been reported. Higher heritability for the aggression-related subscales has been reported in a small sample of Golden Retrievers (Liinamo et al., 2007), however, the dogs in that study were chosen for being aggressive, and their relatives were included as well. Thus, for reliable estimates, large enough random samples are a necessity.

MacLean et al. (2019) estimated considerably higher heritability for the C-BARQ subscales, ranging from 0.27 to 0.77. However, these estimates were based on among-breed variation. Morrill et al. (2022) estimated heritability based on SNP information for various behavior traits based on owner questionnaires. They reported that heritability was greater than 0.25 for the behavioral factors Human sociability (0.67), Toy-directed motor pattern (similar to Playfulness) (about 0.4), and Biddability (similar to Trainability) (about 0.25, estimates only shown in graph). Retrieving was the non-factor trait with the highest heritability, 0.52. However, all these estimates of genetic variation were across all breeds, which would also include the between-breed variation. This was also seen because the breed effect (from a separate ANOVA) was strongly correlated with the heritability estimate (0.89). Therefore, the heritability estimates from both these two studies are difficult to compare with our, within-breed, heritability.

The variance ratios for rater showed that there was more disagreement among raters for Sociability and Aggressiveness than for

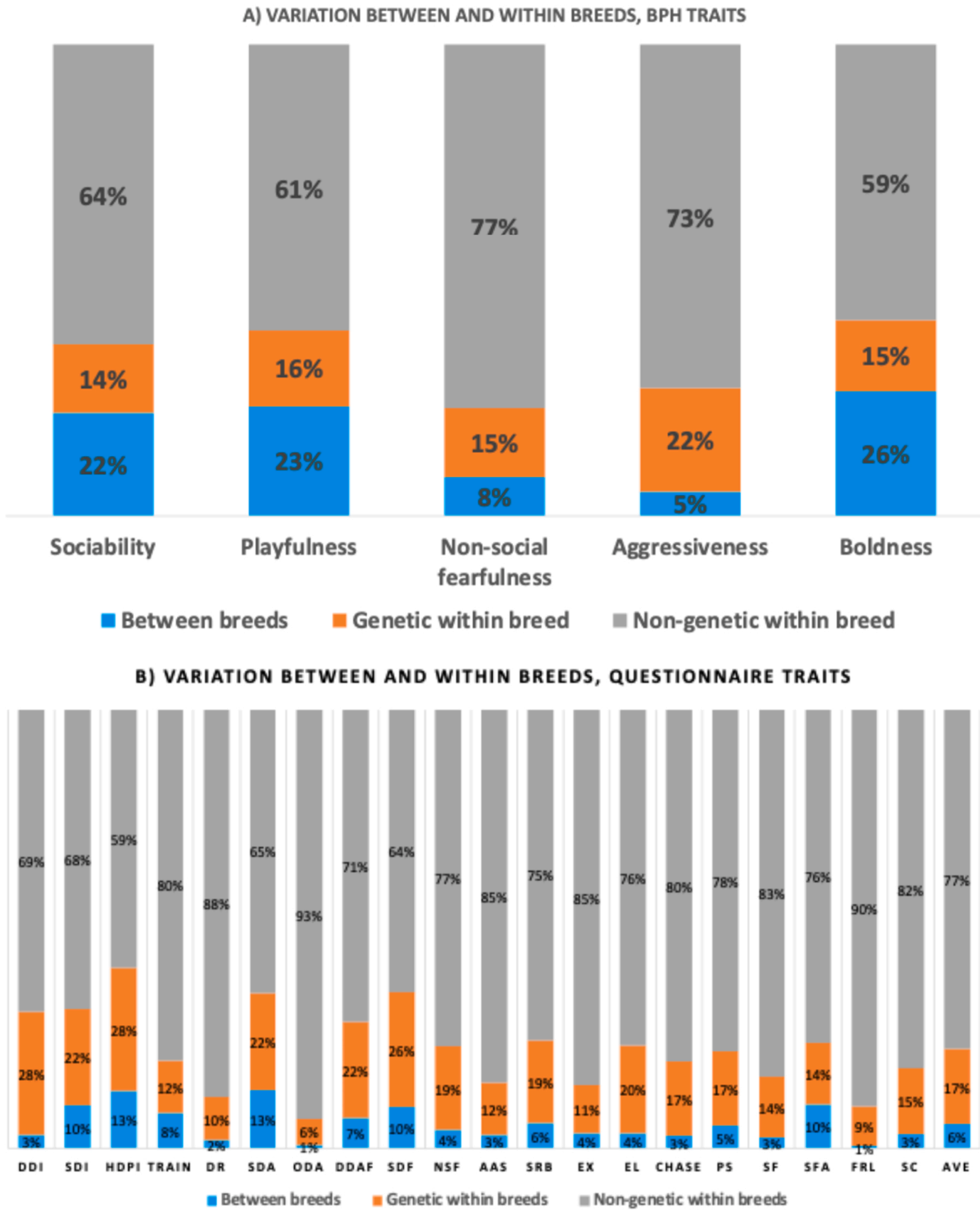

Fig. 3. Proportion of variance attributable to between breeds, genetic within breeds, and non-genetic causes across eight breeds for A) BPH traits, B) questionnaire traits (DDI: Dog-directed interest, SDI: Stranger-directed interest, HDPI: Human-directed play interest, TRAIN: Trainability, DR: Dog rivalry, SDA: Stranger-directed aggression, ODA: Owner-directed aggression, DDAF: Dog-directed aggression or fear, SDF: Stranger-directed fear, NSF: Non-social fear, AAS: Attachment and attention seeking, SRB: Separation-related behavior, EX: Excitability, EL: Energy level, CHASE: Chasing, TS: Touch sensitivity, SF: Situational fear, SFA: Social fear and aggression, FRL: Fear recovery latency, SC: Stubborn and curious, AVE: Average across all traits.

Playfulness and Non-social fearfulness. There was also much less difference in these variance ratios between breeds for these latter two traits. This indicates that it is easier to evaluate Playfulness and Non-social fearfulness consistently and that the breeds show similar reactions to these situations. This is somewhat contradictory to the results from a study of interrater agreement of the BPH raters presented in Svartberg (2021). Among the traits analyzed in this study, Aggressiveness had the highest agreement estimates in that study, whereas the raters were least in agreement for Playfulness. However, the rate agreement study was done in 2016, only four years after BPH was launched. At that time, there were fewer raters, and they had been trained by the founders of the BPH. The data in this study were collected from a larger number of raters who were educated at a later stage, when more experience had been gathered. Furthermore, it seems that it is more difficult to correctly identify Aggressiveness for some breeds (e.g., Perro de Agua Español), whereas there was good agreement between raters for American Staffordshire Terrier. This indicates that breed-typical ways of expressing behavioral reactions rated in the BPH, especially threatening behavior, should be highlighted in the training of the raters.

4.2. Estimates of genetic correlation

The general correlation pattern between the studied BPH traits – a positive genetic correlation between Playfulness and Sociability, and negative correlations between these traits and Non-social fearfulness – supports previous findings of Boldness as an underlying broad trait (Svartberg, 2021). A similar correlation pattern has also been found in the DMA (Svartberg and Forkman, 2002). In the current study, however, Aggressiveness was genetically negatively correlated with Boldness, Sociability, and Playfulness and positively correlated with Non-social fearfulness (Table 3), something that is generally not found in the DMA, phenotypically (Svartberg and Forkman, 2002; Svartberg, 2005; Saetre et al., 2006). Indeed, even a positive genetic correlation was found between Playfulness or Curiosity/fearlessness and Aggressiveness in German Shepherd Dogs and Rough Collie (Strandberg et al., 2005), whereas we found correlations in the opposite direction.

In a phenotypic comparison between DMA and BPH traits, somewhat different correlation pattern was found for Aggressiveness from the two assessment types (Svartberg, 2022), not only with other traits from DMA and BPH, which were in line with what we found here, but also with aggressiveness in everyday life. The results indicated that BPH Aggressiveness, compared with DMA Aggressiveness, is more closely associated with hostile attitude towards strangers outside the test. This may be due to the different methods of measuring aggressive reactions in the two assessments, and that the approaching person(s) in the two assessments, the type of stimulus that elicits most aggressive reactions in the assessments, are differently dressed; in the DMA as non-person like 'ghosts', and in the BPH as an oddly looking stranger.

Using the 1078 dogs of Svartberg (2022) that had been assessed in both DMA and BPH, Aggressiveness in DMA was basically uncorrelated with Sociability, Playfulness, and Boldness. In contrast, the correlation of these latter traits with Aggressiveness as defined in BPH was around −0.20. It seems that Aggressiveness is the trait that is most differently defined between DMA and BPH. The other traits, Sociability, Playfulness, Non-social fearfulness (Curiosity/fearlessness in DMA), and Boldness had phenotypic correlations between 0.47 and 0.59 between DMA and BPH, however, the correlation for Aggressiveness was only 0.25.

Another contributing reason for the different correlations with Aggressiveness could be that the relationship between traits is different for the breeds used in Strandberg et al. (2005), or possibly for working dog breeds in general. Using the 1078 dogs of Svartberg (2022) that had been assessed in both DMA and BPH, we could see that Aggressiveness from DMA was phenotypically uncorrelated with everything else for both working dogs and other dogs (from zero to |0.10|. Aggressiveness from BPH was slightly less negatively correlated with Sociability and Boldness in working dogs (approx. −0.17) than in non-working dogs (approx. −0.23).

Some differences in correlations were found between breeds in our study. For example, Labrador Retriever, Lagotto Romagnolo, and Nova Scotia Duck Tolling Retriever had rather low, or even slightly negative, genetic correlations between Sociability and Playfulness. Breed differences in correlation patterns between DMA traits have previously been identified. Sundman et al. (2016) found that similar selection criteria – hunting or companion/show – in two retriever breeds were nevertheless related to different DMA behavior patterns in the two breeds, which may indicate that the genetic architecture related to behavior differs between breeds. Furthermore, prosocial traits (DMA Playfulness and Sociability) and reactive traits (DMA Aggressiveness and Fearfulness, based on two measures of fear), respectively, were more correlated in ancient breeds than in modern breeds (Hansen Wheat et al., 2019). Even though our selection of breeds does not allow for such a comparison (all breeds in our study are to be considered modern), the difference in correlation pattern strengthens the suggestion that the genetic architecture may differ between breeds and that different or even similar selection criteria may result in different behavior profiles in different breeds.

One finding related to the genetic correlations between traits was that there seems to be a relation between the degree of correlations and the degree of heritability estimates. This relates to the correlations between the three most highly Boldness-related traits – Playfulness, Sociability, and Non-social fearfulness. High intercorrelations for these traits (with reversed signs for Non-social fearfulness) seem to go hand in hand with high heritability for Boldness. Thus, in breeds with higher correlation between the traits, most obvious in the Rhodesian Ridgeback with an intercorrelation of 0.51, the heritability was higher (0.38), whereas in breeds where the traits are more decoupled, as in American Staffordshire Terrier and Lagotto Romagnolo (with intercorrelations of 0.06 and 0.09, respectively), the heritability estimates for Boldness ws low (0.12 and 0.13, respectively). This indicates that for a higher-order trait like Boldness, one prerequisite for high heritability is good internal consistency, i.e., high correlations between the narrower aspects of the higher-order trait. However, the average heritability of the three Boldness-related traits was also related to the heritability of Boldness. For instance, for American Staffordshire Terrier and Lagotto Romagnolo, the average heritability was 0.16–0.17, whereas for Rhodesian Ridgeback, the average heritability was 0.27.

In working dogs, using DMA, Strandberg et al. (2005) and Arvelius et al. (2014) found positive genetic correlations between Playfulness and Curiosity/fearlessness of 0.57 and 0.47, respectively. This is stronger than our correlation of −0.19 between Playfulness and Non-social fearfulness, with an opposite sign, as expected. Arvelius et al. (2014) found a strong genetic correlation between Sociability and Playfulness of 0.69, stronger than our average correlation of 0.31 and stronger than that for any of our breeds. One reason for the difference could be that the traits are measured differently in DMA and BPH. Among the dogs of Svartberg (2022) that had been assessed in both DMA and BPH, the phenotypic correlation was weaker between Playfulness and Non-social fearfulness from BPH (-0.24) than the corresponding correlation with Curiosity/fearlessness from DMA (0.47). However, the correlation between Sociability and Playfulness was only slightly higher in DMA (0.30) than in BPH (0.25).

For the genetic correlations between BPH traits and everyday behavior traits defined from the questionnaire, we found strong and consistent correlations where it was expected (Table 5). For instance, Sociability had the strongest correlation with Stranger-directed interest (0.93) and Stranger-directed fear (-0.89), but also with the newly defined Social fear and aggression (-0.81). This aligns with a similar study on Rough Collie, where everyday behavior was compared with DMA traits (Arvelius et al., 2014). Playfulness was, as expected, positively correlated with Human-directed play interest (0.77) but also with Energy level (0.52) and Trainability (0.48), which is higher than the results of Arvelius et al. (2014). This could be due to different samples, but because it is in line with phenotypic correlations (Svartberg, 2005, 2021), BPH Playfulness may be a better indicator for the dog's Trainability and Energy level in everyday life than the corresponding trait from DMA. Also as expected from previous results, Non-social fearfulness was strongly correlated with Non-social fear (0.77), as well as with the new traits Situational fear (0.88) and Fear recovery latency (0.80). The correlations with Aggressiveness were somewhat lower, with the highest correlation with Stranger-directed aggression (0.57), which is, however, greater than what has been found in the DMA. This further strengthens the suggestion that the Aggressiveness trait in BPH is a better predictor for everyday behavior than DMA Aggressiveness.

There were also other strong and consistent genetic correlations for trait pairs where the BPH subtest situation did not clearly match the questions included in the questionnaire trait. For instance, there is no situation in BPH in which dog-dog interactions are assessed. Nevertheless, there were consistent correlations, e.g., for Sociability with Dog-directed interest, Dog rivalry, and Dog-directed aggression or fear. Even though this connection has been found previously in DMA (Arvelius et al., 2014), the correlations to dog-related questionnaire scales are higher in BPH, overall. This difference was previously found at a phenotypical level (Svartberg, 2021). It suggests that the dog's social attitude towards unfamiliar persons and unfamiliar dogs have a common denominator that, at least to some degree, is captured by BPH Sociability.

4.3. Variation between and within breeds

We found several significant breed differences for both BPH traits and questionnaire subscales. Even more striking, however, was the considerable variation within breeds for all traits and subscales, and that all distributions overlapped, even those for top- and bottom-ranked breeds. One example is BPH Playfulness, where one of the largest breed differences was obtained between Labrador Retriever and Lagotto Romagnolo. Despite the breed difference, about 11 % of the Lagotto Romagnolo had as high or higher Playfulness score than the average Labrador Retriever. The fact that within-breed variation for most traits and subscales was greater than between-breed variation suggests that this also applies to genetic behavioral variation. This has been highlighted previously for DMA traits (Svartberg, 2006), and more general by Scott and Fuller (1965) in their study, who reported considerable variation in behavior between individual dogs, litters, and strains within the studied breeds. More recently, Morrill et al. (2022) found high behavioral variability within breeds, and stated that breed may affect the likelihood of a particular behavior but that no behaviors are exclusive to a breed or a subset of breeds.

It is possible that some behaviors may vary more between individuals than between breeds and vice versa. The BPH trait with the lowest between-breed variation was Aggressiveness. This trait seems to correspond to "Agonistic threshold" in Morrill et al. (2022), which was the behavioral factor with the lowest proportion between-breed variation. Also, two of the aggression-related subscales – Dog rivalry and Owner-directed aggression – had very low between-breed variation. Besides the higher-order trait Boldness, Playfulness was the BPH trait with the highest between-breed variation. This also applies to the corresponding subscale Human-directed play interest, which was the one among the questionnaire subscales with the highest variation between breeds. Morrill et al. (2022) reported the largest between-breed variance in "Toy-directed motor patterns", a behavioral factor highly similar to Playfulness and Human-directed play interest. Thus, toy play could be a dog behavior that varies more between breeds than between individuals within a breed. However, all comparisons do not fit the pattern; more results are needed to shed light on how different behaviors vary between and within breeds.

The genetic variation between breeds was more pronounced for BPH traits, especially for Sociability, Playfulness, and Boldness (22–26 %), than for questionnaire traits (average 6 %). Morrill et al. (2022) estimated the between-breed proportion of variance to be around 9 %. This difference may be due to the data collection method, since Morrill et al. (2022) based their results on questionnaire data. It is possible that behavioral reactions in a provoked situation, as in the BPH subtests, may reveal more breed-typical differences compared with questionnaire responses. Scott and Fuller (1965), who based their results on behavior tests, reported that the between-breed variance was often considerably greater than within breeds. In the questionnaire, the respondent describes the dog's typical reactions in a range of everyday situations that may give a slightly different result, which, to some degree, downplays differences between breeds.

4.4. Strengths and limitations of the study

Even though we have a large enough number of observations for estimating heritability and genetic correlation among BPH traits, the amount of data for estimating the genetic correlation between BPH traits and the questionnaire traits is still a bottleneck. Ideally, all BPH records would be accompanied by a questionnaire response. In the ongoing development of routine genetic evaluation for BPH traits, breed clubs encourage their breeders (who in turn contact their puppy buyers) to increase the questionnaire response rate to better validate the results before publishing estimated breeding values for the breeds.

In this study, genotypes of animals were not available. For practical breeding purposes, this is of minor consequence because the dogs are not used for breeding earlier than the recommended age for BPH. Thus, we can present pedigree-based breeding values for selection purposes. However, although we have more precise measurements of behavior than using questionnaire data, we are unable to find underlying genetic causation for the difference in behavior between dogs within a breed or between breeds.

5. Conclusions

Heritabilities for BPH traits were generally high enough to make selection feasible, with sufficient accuracy. There was a reasonable heritability for most traits defined from the questionnaire, indicating the existence of genetic variation also in these traits. However, for some breeds, some estimates converged to zero, probably owing to too few observations. The scarcity of questionnaire data also affected the possibility of estimating genetic correlations between BPH and questionnaire traits. Nevertheless, consistently positive or negative genetic correlations were found for trait pairs where we would expect a strong correlation, e.g., between Sociability and Stranger-directed interest. Often, we could also see that a measure at BPH involving interactions with humans also extended to measure reactions to interactions with other dogs, e.g., a strong genetic correlation between Sociability and Dog-directed interest. In summary, selecting dogs based on traits defined at BPH is expected to result in behavioral changes not only when measured at BPH but also changes in everyday behavior in an expected way. However, there is a need for continued data collection to increase the number of questionnaire answers, especially in the breeds where the statistical analysis failed to converge.

Declaration of Competing Interest

The author KS was one of the developers of the BPH and acted during the development process as a consultant for the Swedish Kennel Club.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.applanim.2025.106619.

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