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Similar recent selection criteria associated with different behavioural effects in two dog breeds

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Selection during the last decades has split some established dog breeds into morphologically and behaviourally divergent types. These breed splits are interesting models for behaviour genetics since selection has often been for few and well-defined behavioural traits. The aim of this study was to explore behavioural differences between selection lines in golden and Labrador retriever, in both of which a split between a common type (pet and conformation) and a field type (hunting) has occurred. We hypothesized that the behavioural profiles of the types would be similar in both breeds. Pedigree data and results from a standardized behavioural test from 902 goldens (698 common and 204 field) and 1672 Labradors (1023 and 649) were analysed. Principal component analysis revealed six behavioural components: curiosity, play interest, chase proneness, social curiosity, social greeting and threat display. Breed and type affected all components, but interestingly there was an interaction between breed and type for most components. For example, in Labradors the common type had higher curiosity than the field type ($F_{1,1668} = 18.359$; $P < 0.001$), while the opposite was found in goldens ($F_{1,897} = 65.201$; $P < 0.001$). Heritability estimates showed considerable genetic contributions to the behavioural variations in both breeds, but different heritabilities between the types within breeds was also found, suggesting different selection pressures. In conclusion, in spite of similar genetic origin and similar recent selection criteria, types behave differently in the breeds. This suggests that the genetic architecture related to behaviour differs between the breeds.

Keywords: Behavioural genetics, behavioural test, dog behaviour, dogs, golden retriever, heritability, Labrador retriever, selection

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The dog is the oldest domesticated animal and has lived with humans for at least 14.000 years (Freedman *et al.* 2014; Skoglund *et al.* 2015; Thalmann *et al.* 2013). Over this time, various types of dogs have developed through adaptation to an environment shared with humans and selective breeding, resulting in a unique within-species variation in morphology and behaviour. The stringent selective breeding we are familiar with today began with the founding of breeding associations and breed standards in the 19th century, giving rise to purebreds with closed gene pools (Boyko 2011; Parker *et al.* 2004). Behavioural variation between breeds is immense with respect to breed-specific behaviours such as herding in border collies and retrieval of game in Labrador retrievers, but is also remarkable in behavioural traits such as boldness, playfulness, sociability and aggression (Duffy *et al.* 2008; Starling *et al.* 2013; Svartberg 2006). There is a substantial genetic basis for the variation in behaviour, as estimated by heritability (Saetre *et al.* 2006; Scott & Fuller 1965). The combination of closed populations and selection, intentional as well as unintentional, for different behaviour profiles between breeds makes dogs excellent subjects for studies of the genetic foundation for behaviour.

While most breeds have been genetically separated for a relatively long time, within-breed divergence has occurred more recently in some. For example, in the closely related breeds golden and Labrador retrievers diversification has occurred due to different selection criteria applied to dogs within the same breed. The original function of both breeds was to retrieve game and historically selection has focused on this function. In response to conformation shows and retrievers becoming popular pet dogs during the 1970s, a divergence in selection goals occurred resulting in two distinct types within each breed: the common type, primarily bred for conformation, and the field type, bred for hunting. A study on Labrador retrievers found differences between pet, show and gundogs in several behaviours, for example fetching and trainability (Lofgren *et al.* 2014), demonstrating behaviour differences between types.

These breed types, which have very recently diverged from a common gene pool, are particularly interesting from the perspective of behaviour genetics. Firstly, the types within each breed have a similar genetic background and selected genes affecting the behavioural differences should stand out against it. Additionally, similar behavioural differences within the two breeds may provide indications concerning the genetic architecture of behavioural traits, especially when concerning behaviours not directly targeted by selection. If the same trait complexes differ in the same way between selection lines in both breeds, this would indicate a similar architecture. Even though not directly targeted by selection, we would expect the traits to have been affected similarly due to underlying genetic mechanisms such as linkage or pleiotropy.

In this study we explore the differences in behaviour between golden and Labrador retriever and the within-breed differences between the two selection lines by using behavioural data from the Swedish Dog Mentality Assessment (DMA). We hypothesise that there will be similar behavioural differences between types in both breeds. We also calculate the heritabilities for the behavioural traits found in the populations.

Materials and methods

Animals

We used behavioural data from golden retrievers ('goldens') and Labrador retrievers ('Labradors') tested in the DMA (described below) between 1 January 2005 and 15 February 2014 in Sweden. To classify the dog as being either common type or field type, pedigree data was used and the ancestry of the dogs was traced. To be classified as a field-type retriever, the dog had to have a pedigree that consisted of field-bred dogs for at least three generations. This was based on field-trial titles in and beyond the three generations. If none of the dogs in the three previous generations were bred for field work, they were classified as common-type retrievers. These dogs had instead ancestors with show titles. Those dogs with an ancestry that consisted of both types were classified as mixed and not included in further analyses. Pedigrees were found mainly through the Swedish Kennel Club's online registry (Hunddata, http://hundar.skk.se/hunddata/), but also the database k9data.com (http://www.k9data.com/) that contains pedigrees of goldens and Labradors from different registries, for example the Kennel Club of Great Britain. The vast majority of the dogs included in the behavioural tests were born and raised in Sweden, but the original ancestry of all goldens and Labradors in Sweden, regardless of type, is Great Britain.

For goldens, the pedigrees of 1445 dogs were analysed, of which 698 were common type (330 females and 386 males) and 204 were field type (101 females and 103 males). Mean age in days at behavioural testing for the common type was 705.29 ± 11.11 (779.03 ± 20.87 for females and 711.79 ± 15.85 for males; SEM) and for the field type it was 575.44 ± 18.22 (625.32 ± 32.70 for females and 527.47 ± 15.79 for males; SEM). For Labradors, the pedigrees of 1965 dogs were analysed, and 1023 of these were common type (567 females and 456 males) whereas 649 were field type (292 females and 357 males). Mean age in days at behavioural testing for the common type was 761.87 ± 12.05 (760.73 ± 16.22 for females and 763.29 ± 18.02 for males; SEM) and for the field type it was 650.36 ± 12.48 (654.85 ± 19.00 for females and 646.69 ± 16.54 for males; SEM). Two hundred and eighty-four Labradors and 543 goldens had a mixed pedigree and thus not included. A majority of the dogs of both breeds and both types were born in the first two quartiles of the year and participation in the DMA followed an equal distribution between types in both breeds across the year (Figs. S1 and S2, Supporting Information). Hence, season of test did not differ systematically between the dog groups.

Dog Mentality Assessment

The DMA is a standardized behavioural test developed as a tool by the Swedish Working Dog Club for breeding assessment of working dogs, but it is also used as a general behavioural test for many dogs of most breeds in Sweden. Since 1997 more than 100 000 dogs have been tested. The DMA is a test battery where the behaviours are measured with behavioural rating. It consists of 10 subtests where the dogs' reactions are evaluated on an intensity scale (1–5) for 33 behavioural variables. Judge, test leader and other personnel are trained and certified by the Swedish Working Dog Club. Subtests are shortly described in Table 1 and the full protocol with behaviour scores is provided in Table S1. The dogs have to be at least 1 year old to participate. The reliability and validity of the DMA has been extensively ascertained (Svartberg 2002, 2005; Svartberg & Forkman 2002; Svartberg *et al.* 2005). For a thorough description of the test, see Svartberg and Forkman (2002).

Statistical analysis

We first used principal component analysis (PCA) to reduce the 33 variables of the DMA data on the total sample of dogs, $n = 2574$. Sampling adequacy: Bartlett's sphericity test $\chi^2 = 22963.962$, df = 528, $P < 0.001$; Kaiser-Meyer-Olkin Measure of Sampling Adequacy: 0.767. The PCA was rotated with varimax rotation. We then used the individual PC scores in further analyses. General Linear Models (GLM) were used to analyse the effect of breed and type on the components. Sex, test year and season of birth (fixed factors) as well as age in days (covariate) were also added to the models to account for possible effects of these. Season of birth and test year did not have a significant effect for any of the components and were therefore removed from the models and are not presented. The software IBM SPSS STATISTICS 23 was used for all statistical analysis. Results are presented as mean ± SEM.

Heritability estimates

We estimated narrow sense heritability for each principal component score with quantitative genetic animal models (Kruuk 2004). We performed Bayesian inference with Markov Chain Monte Carlo in the R statistical environment (R Core Team, 2014) with the MCMCglmm package (Hadfield 2010). Heritability was calculated as the ratio of the additive genetic variance to the total variance. We used a parameter expanded prior (Gelman 2006) for the additive genetic variance component with $V = 1$, $\nu = 1$, $\alpha_\mu = 0$, $\alpha_V = 1000$, which corresponds to a half-Cauchy prior with scale 100. For the residual variance component, an inverse-Wishart prior ($V = 1$, $\nu = 0.002$) was used. The half-Cauchy prior is less informative than the inverse-Wishart when the variance component is small. Models also included age and sex as fixed covariates with diffuse normal priors. For the quantitative genetic analysis, we used pedigree files provided by the Swedish Kennel Club. We only kept the individuals informative for relatedness. For the golden dataset, this resulted in a total of 5598 individuals, of which 4278 of the common type and 1418 of the field type, and for the Labrador dataset a total of 7810 individuals, of which 4858 of the common type and 3289 of the field type. We ran each model for a total of two million iterations. Because of the size of the dataset we used parallel computation, using mclapply from the parallel package, to speed up calculations. We ran 20 chains for the combined breed datasets and 60 for the smaller datasets of separated breed types, each of 100 000 iterations. Each chain had 3000 burn-in samples that were discarded. The thinning interval was 100. Convergence was tested with Heidelberg and Welsh's diagnostic.

Results

Based on a combination of eigenvalues and the shape of the scree plot, six principal components were retained from the PCA. The scree plot is provided in Fig. S3. Together they explained 45.8 % of the total variance. The PCA loadings with percentage of variance for each component are shown in Table 2. Variables that loaded >0.3 were considered of relevance for a particular component and 31 of the 33 variables fulfilled this for at least one of the six components. The components were tentatively named based on the relevant variables. Of relevance for the first component were variables regarding curiosity (positive loadings) and avoidance behaviour (negative loadings). Therefore, this component was named curiosity. The second component showed high loadings for variables regarding play and was named play interest. Variables from the subtest chase were of relevance for the third component and it was named chase proneness.

Table 1: A description of the 10 subtests of the Dog Mentality Assessment

Subtests	Description
1. Social contact	A stranger (test leader, TL) greets the dog, takes the lead and walks away from the owner and finally handles the dog. Dog's greeting intensity, willingness to follow and engage and willingness to be handled are scored.
2. Play 1	TL and owner throws a toy between them and then throws it on the ground, TL then invites the dog for tug-of-war. How quickly and intensely the dog begins to play, if and how it grabs the toy and how intensely it engages in tug-of-war are scored.
3. Chase	A prey-like toy is pulled in a zigzag pattern across the ground. Dog's willingness to chase and grab are scored. This subtest is done twice.
4. Passive situation	Owner stands passive with the dog on a long leash for three minutes. Dog's activity is scored.
5. Distance play	A stranger with cape and hood walks 40 meter in front of the dog acting threatening. The hood is removed and a toy is tossed. The stranger goes to a hiding place where the cape is removed and calls for the dog, which is let go. The stranger comes out of the hiding place and invites the dog to play. Dog's interest in the stranger and threat intensity are scored in the first part when the dog is on the leash; willingness to go out to the stranger (curiosity), tug-of-war intensity and willingness to cooperate with the stranger are scored in the second part.
6. Visual startle	A boiler suit is rapidly pulled up in front of the dog. Intensity of startle reaction, threat behaviour and the dog's willingness to investigate (curiosity) are scored. When the dog has investigated, walks are taken past the boiler suit and avoidance behaviour and interest are scored.
7. Sound startle	A metal chain is pulled of corrugated metal when the dog walks past. Intensity of startle reaction and the dog's willingness to investigate (curiosity) are scored. When the dog has investigated, walks are taken past the place where the sound occurred and avoidance behaviour and interest are scored.
8. Ghosts	Two strangers covered in white cloth from head to toe, the hood with eyes in black painted on it, walks slowly closer and closer towards the dog from different directions. Threat behaviour, attention, avoidance behaviour, willingness to approach (curiosity) and social contact behaviour are scored.
9. Play 2	As Play 1.
10. Gunshot	Four gunshots are fired, two during activity (tug-of-war or running with owner) and two during passivity. Dog's avoidance behaviour is scored.

The fourth and fifth components had high loadings of different social behaviours and were called social curiosity and social greeting, respectively. Finally, threatening behaviour in different subtests were of relevance to the sixth component, which was therefore called threat display. The principal components are from this point referred to by those names.

Differences between and within breeds are shown in Fig. 1 and F and P values of the main factors and the breed × type interaction are shown in Table 3. Firstly, breed had a significant effect on all of the six components, where Labradors showed higher curiosity, play interest and threat display and goldens higher chase proneness, higher social curiosity and higher social greeting. Additionally, type had a significant effect on all components. However, in four of the components, namely curiosity, play interest, social curiosity and social greeting, there was a significant interaction between breed and type. For chase proneness, there was a trend for an interaction between breed and type. Thus, the effect of type on the components differed depending on breed. Within the goldens, field-bred dogs had higher curiosity ($F_{1,897} = 65.201$; $P < 0.001$), play interest ($F_{1,897} = 46.146$; $P < 0.001$), chase proneness ($F_{1,898} = 17.807$; $P < 0.001$) and social greeting ($F_{1,897} = 9.097$; $P = 0.003$), while there was no difference between the types in social curiosity. Within the Labradors, field-bred dogs had a higher play interest ($F_{1,1668} = 18.359$; $P < 0.001$) while common-bred dogs had higher curiosity ($F_{1,1668} = 29.855$; $P < 0.001$), social curiosity ($F_{1,1668} = 28.532$; $P < 0.001$) and social greeting ($F_{1,1668} = 116.955$; $P < 0.001$). Chase proneness did not differ significantly between the types within Labradors.

Sex affected five of the behaviour components. Males had higher curiosity (0.040 ± 0.028 vs. -0.040 ± 0.026), had a higher play interest (0.102 ± 0.026 vs. -0.101 ± 0.027), showed higher social curiosity (0.114 ± 0.027 vs. -0.113 ± 0.026) and social greeting (0.055 ± 0.027 vs. -0.055 ± 0.026), but had lower threat display (-0.064 ± 0.027 vs. 0.063 ± 0.026). For play interest, there was a three-way interaction between breed, type and sex ($F_{1,2565} = 8.250$; $P < 0.001$). While there was no interaction between type and sex in goldens, there was one in Labradors ($F_{1,1667} = 8.157$; $P = 0.004$). There was no difference between the sexes in the common type, but in field-typed Labradors, males had higher play interest (0.384 ± 0.045 vs. 0.137 ± 0.053; $F_{1,646} = 13.024$; $P < 0.001$).

Concerning the age of the dogs, it had a significant effect on all six components. Curiosity increased with age, while the other behavioural components decreased with age. The absence of interactions between age and the other factors indicates that age does not explain differences in type.

Heritability calculations and their highest posterior density (HPD) credible interval for breeds and types within breeds are presented in Table 4. The heritabilities were substantial for the six traits in both goldens and Labradors as well as for a majority of the traits when the data set was further split into types. Due to smaller sample sizes in the calculations of the latter, some of the lower ends of the 95% HPD

Table 2: The result of the principal component analysis. Variables >0.3 (in bold) were considered of relevance to each component

Behavioural variables	PC1	PC2	PC3	PC4	PC5	PC6
1a. Contact, greeting	0.026	0.104	0.065	0.074	**0.716**	0.041
1b. Contact, co-operation	0.011	0.132	0.032	−0.026	**0.702**	−0.010
1c. Contact, visitation	0.056	0.132	−0.003	0.116	**0.700**	−0.049
2a. Play 1, play interest	0.050	**0.668**	0.113	0.103	**0.308**	0.090
2b. Play 1, grabbing	0.124	**0.707**	0.060	0.033	0.077	0.006
2c. Play 1, tug-of-war	0.093	**0.570**	0.063	0.297	0.106	0.021
3a 1. Chase	0.042	−0.036	**0.781**	0.124	0.054	0.039
3a 2. Chase	−0.016	0.042	**0.805**	0.066	0.056	0.021
3b 1. Grabbing	0.112	0.105	**0.768**	0.078	0.020	−0.021
3b 2. Grabbing	0.094	0.195	**0.757**	0.019	0.009	−0.010
4. Passive situation	−0.019	0.063	0.058	0.027	0.222	0.181
5a. Distance play, interest	0.024	0.079	0.039	0.391	0.003	0.273
5b. Distance play, threat	0.051	0.062	−0.146	−0.129	−0.002	**0.526**
5c. Distance play, curiosity	0.070	0.053	0.137	**0.803**	0.080	−0.028
5d. Distance play, play interest	0.077	**0.316**	0.101	**0.802**	0.100	−0.005
5e. Distance play, cooperation	0.074	0.230	0.073	**0.770**	0.093	0.016
6a. Visual surprise, startle reaction	**−0.675**	−0.058	0.049	−0.087	−0.015	0.121
6b. Visual surprise, threat	−0.085	−0.039	0.019	0.038	−0.015	**0.609**
6c. Visual surprise, curiosity	**0.731**	0.053	0.037	0.096	0.024	−0.050
6d. Visual surprise, remaining avoidance	**−0.691**	−0.117	0.000	−0.061	−0.027	0.050
6e. Visual surprise, remaining interest	−0.074	0.121	0.129	0.030	0.081	0.225
7a. Sudden noise, startle reaction	**−0.663**	−0.043	−0.110	0.006	−0.020	−0.117
7b. Sudden noise, curiosity	**0.609**	0.094	0.169	−0.073	0.040	0.194
7c. Sudden noise, remaining avoidance	**−0.596**	−0.122	−0.096	0.047	−0.024	−0.120
7d. Sudden noise, remaining interest	−0.044	0.090	0.161	−0.012	0.026	0.233
8a. Ghosts, threat	0.193	−0.078	−0.050	0.008	−0.062	**0.701**
8b. Ghosts, control	0.114	−0.063	−0.012	0.143	0.029	**0.551**
8c. Ghosts, avoidance	**−0.383**	0.046	0.091	−0.205	0.012	0.236
8d. Ghosts, curiosity	**0.438**	−0.110	−0.050	**0.330**	0.211	−0.104
8e. Ghosts, greeting	**0.341**	−0.082	−0.034	0.290	**0.399**	−0.034
9a. Play 2, play interest	0.106	**0.756**	0.111	0.125	0.117	0.030
9b. Play 2, grabbing	0.166	**0.781**	0.037	0.084	−0.013	−0.017
10. Gun shot	**−0.338**	−0.171	0.026	−0.018	0.025	−0.095
% of variance	10.34	8.64	7.98	7.59	5.82	5.56

interval were close to 0 (<0.001) and thus the heritability could not be separated from 0. Considering those traits with no or minimal credible interval overlaps, the heritability differed clearly between the breeds for the trait play interest, between types within goldens for chase proneness and between types within Labradors for curiosity.

Discussion

Our results show that the behavioural traits measured by the DMA differed between goldens and Labradors as well as between the selection lines within breeds. Behavioural reactions in the DMA could be reduced to the six components curiosity, play interest, chase proneness, social curiosity, social greeting and threat display, which is similar to what was previously found in DMA data (Svartberg & Forkman 2002). Goldens and Labradors as well as selection lines differed on all six components. Importantly, there was also an interaction between breed and type for most components, showing that in spite of a similar genetic origin and similar recent selection criteria, the behavioural differences between types are not consistent in the two breeds. A considerable genetic contribution to the traits is obvious from the heritability estimates, and the variation in heritability across breeds and types indicates a difference in selection pressures. Moreover, sex and age had considerable effects on several components.

The two breeds (goldens and Labradors) have a relatively recent common ancestor and the types, of course, have an even more recent joint ancestry within breeds. Both hunting types have mainly been selected for retrieving and endurance, while the common types of both breeds have been selected as family and show dogs (Duffy *et al.* 2008; Lofgren *et al.* 2014). We therefore hypothesized that the behavioural differences between the selection lines should be similar in goldens and Labradors, showing common side-effects of selection. This was, however, not the case in our study. While there was a significant difference between types for all traits, five of the traits showed a significant interaction between breed and type. Thus, behavioural differences between the types were not necessarily the same in the two breeds. For example, for curiosity and social greeting the field-type Labradors had lower scores than the common type while the opposite was observed for goldens. Similarly,

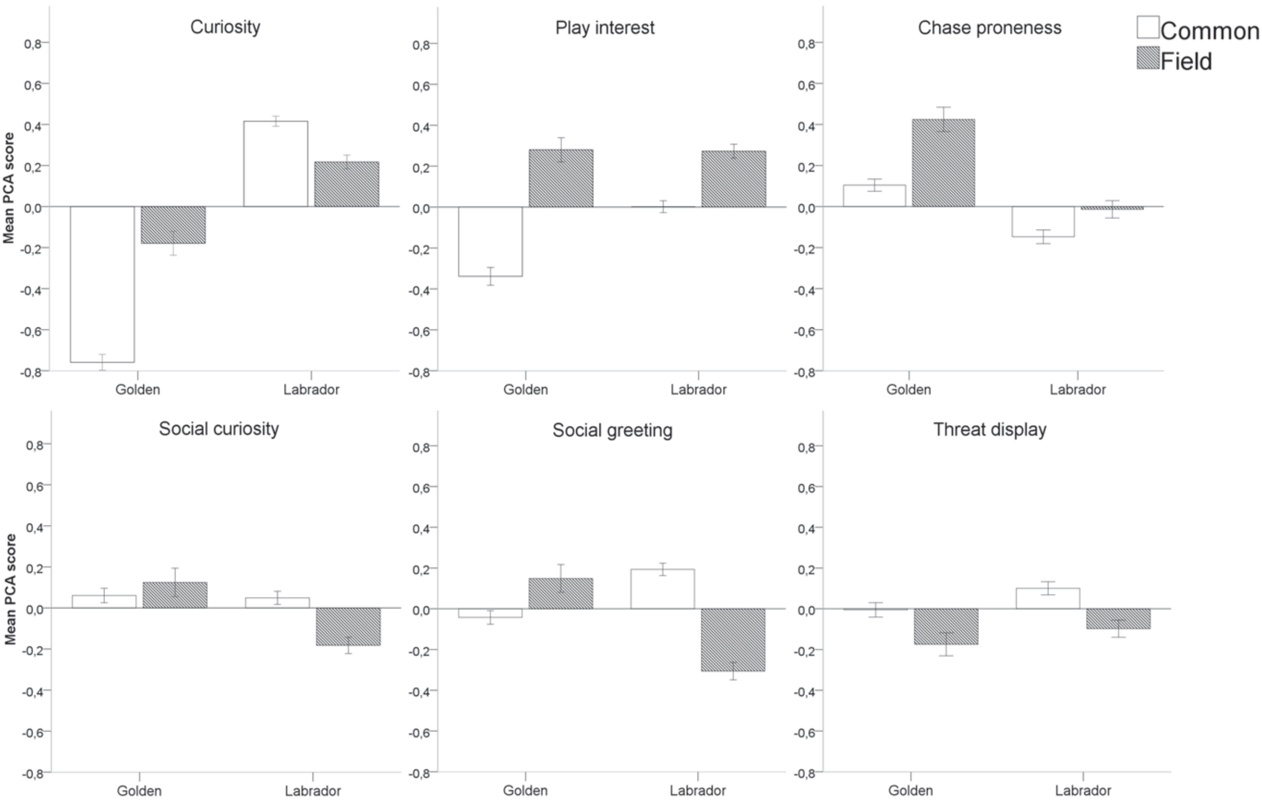

Figure 1: Differences in behaviour between and within breeds. Average principal component scores (PCA score) for breeds (golden and Labrador retrievers) and types within breeds (common or field types). Error bars show ± 1 SEM.

Table 3: *F* and *P* values from the GLMs for main effects and for breed × type interaction

	Curiosity		Play interest		Chase proneness		Social curiosity		Social greeting		Threat display	
	$F_{1,2568}$	*P*	$F_{1,2565}$	*P*	$F_{1,2567}$	*P*	$F_{1,2568}$	*P*	$F_{1,2565}$	*P*	$F_{1,2567}$	*P*
Breed	360.874	<0.001	14.519	<0.001	49.927	<0.001	10.351	0.001	4.104	0.043	6.334	0.012
Type	31.576	<0.001	86.004	<0.001	13.150	<0.001	5.356	0.021	19.043	<0.001	28.450	<0.001
Sex	16.297	<0.001	24.568	<0.001	-	NS	37.017	<0.001	12.390	<0.001	9.973	0.002
Age	46.251	<0.001	5.727	0.017	56.289	<0.001	3.895	0.049	31.125	<0.001	41.015	<0.001
Breed × type	100.309	<0.001	16.000	<0.001	3.152	0.076	11.756	0.001	56.828	<0.001	–	NS

NS, not significant.

Duffy *et al.* (2008) showed that field-bred English springer spaniel were less aggressive than the show type, while in the Labrador, field typed showed higher owner-directed aggression. The lower sociability and curiosity we found for the field-type Labradors concur with results from Lofgren *et al.* (2014), where Labradors used as gun dogs scored lower on these traits than both pet and show dogs. For play interest, however, the field type of both breeds had higher scores than the common type. This may reflect the common selection focus, since breeding for retrieving could be associated with a general interest in objects and play.

Interestingly, since we found that the behaviour of the selection lines did not differ in a similar fashion in both goldens and Labradors and the heritability estimates differed between types, this may imply that the genetic basis for the behavioural traits differs between breeds. Apparently, selection merely for show/pet qualities and field qualities has not affected behaviour outside the breeding target similarly in Labradors and goldens. Rather, attributes not directly affected by the selection may be determined by different genetic architectures in the two breeds. In concurrence, Van Der Waaij *et al.* (2008) found that genetic correlation between the traits cooperation and hardness was positive in the Labrador and negative in the German shepherd dog.

Our narrow sense heritability estimates showed a substantial genetic contribution to each of the traits in both breeds, and the degree of genetic contribution differed both between and within breeds. There were only small overlaps

Table 4: Heritability estimates of the PCA components displayed as h^2 (95 % HPDI low; high)

	Golden retriever			Labrador retriever		
	Breed	Common type	Field type	Breed	Common type	Field type
Curiosity	0.303 (0.172; 0.453)	0.166 (0.030; 0.373)	0.257 (<0.001; 0.685)	0.323 (0.210; 0.451)	0.177 (0.045; 0.240)	0.542 (0.309; 0.777)
Play interest	0.346 (0.217; 0.494)	0.326 (0.179; 0.504)	0.238 (<0.001; 0.534)	0.127 (0.062; 0.217)	0.001 (<0.001; 0.165)	0.136 (0.033; 0.287)
Chase proneness	0.276 (0.139; 0.404)	0.349 (0.196; 0.550)	0.001 (0.000; 0.250)	0.202 (0.104; 0.311)	0.193 (0.092; 0.332)	0.238 (<0.001; 0.453)
Social curiosity	0.237 (0.109; 0.421)	0.251 (0.092; 0.470)	0.184 (<0.001; 0.572)	0.131 (0.059; 0.256)	0.217 (0.056; 0.425)	<0.001 (<0.001; 0.169)
Social greeting	0.186 (0.043; 0.308)	0.157 (<0.001; 0.319)	0.002 (<0.001; 0.538)	0.208 (0.139; 0.321)	0.190 (0.080; 0.315)	0.001 (<0.001; 0.254)
Threat display	0.388 (0.228; 0.546)	0.375 (0.231; 0.577)	0.001 (<0.001; 0.613)	0.282 (0.189; 0.400)	0.359 (0.210; 0.531)	0.216 (0.088; 0.377)

in the credible intervals for the trait play interest between goldens and Labradors, for chase proneness between common and field type within goldens and for curiosity between the types within Labradors, indicating substantial differences in heritabilities between and within breeds. Although there was a greater overlap in credible intervals for the other components, the means suggest differences in heritabilities between types within both breeds. Heritability estimates are population specific and previous studies have shown considerable differences in heritability between breeds for the same traits (Ruefenacht *et al.* 2002). Since genetic variance and thus heritability estimates are expected to change with extensive selection (Visscher *et al.* 2008), the results suggest that the selection pressures in the common and field type of each breed have differed. Furthermore, overall the estimates were moderate to high in size. Heritability estimates on DMA data has previously been reported in the breeds rough collie (Arvelius *et al.* 2014), Rottweiler and German shepherd dog (Saetre *et al.* 2006; Strandberg *et al.* 2005), and these are in the same range as the ones found in the present study. Earlier genetic correlation calculations have suggested that curiosity, play interest, chase proneness and sociability can be combined into the single trait boldness, which may thus to some extent be related to the same genetic basis (Saetre *et al.* 2006; Strandberg *et al.* 2005). Overall, the heritability estimates show that, in spite of a strong selection pressure on some specific traits, there is relatively high genetic variation for the traits measured in all the different populations. However, they also show that selection pressures have differed between populations. For example, the difference in heritabilities of chase proneness observed between common and field types of golden retriever indicates that the breed types have been exposed to different selection pressures for this trait. This is to our knowledge the first study to compare heritability estimates between selection lines within a dog breed.

It has been discussed whether behavioural breed differences are due to the historical function of the breeds or to recent selection criteria. Svartberg (2006) found no correlation between a breed's original function and breed-characteristic behaviour of the traits found in the DMA. Indeed, in that study Labradors and goldens ended up in different groups in a cluster analysis based on behaviour. Contrary to this, Turcsan *et al.* (2011) found evidence that boldness and trainability are partly due to a breed's original function. In the present study, we used two closely related breeds with the same original function and within each similar recent selection criteria has created two types. Owing to the behavioural differences found and due to the lack of consistency in the behavioural differences between the types of the two breeds, our results suggest that breed differences in general behavioural traits are neither due to historical function nor recent selection but rather due to genetic architecture.

Dog breeds are both genetically distinct and show high phenotypic diversity which make them excellent genetic models (Karlsson & Lindblad-Toh 2008). The fact that many breeds were created through a small number of founders, small effective population size and high inbreeding has resulted in genetic differentiation between breeds. Purebred dogs can, consequently, be assigned the correct breed based on genotype data alone (Parker *et al.* 2004; vonHoldt *et al.* 2010). Although this homogeneity exists within dog breeds, substructures are present in some breeds due to geographic origin and breeding regimes, resulting in different types as evident in goldens and Labradors (Chang *et al.* 2009; Quignon *et al.* 2007). Having belonged to a common gene pool and just recently diverged from it, breed types offer a possibility to study both the effects of recent selection and genetic architectures. Traits that differ between the selection lines should stand out against the similar genetic background and thus allow efficient genetic mapping. This regime has been used by Arnott *et al.* (2015), who found a selective sweep in working kelpie connected to behavioural resilience. In future experiments, we will investigate the genetic background of the presently observed differences between golden and Labrador types.

In conclusion, in spite of behavioural divergence between field and common types of golden retrievers and Labrador retrievers, the differences between types were not consistent in the two breeds. This suggests, contrary to what was expected, that the genetic architecture related to behaviour differs between the breeds. The heritability estimates show considerable contributions of genetic factors to the behavioural differences for the traits found in each breed, but we also found a variation within the breeds. This implies a difference in genetic variance because of different selection pressures in the selection lines.

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Supporting Information

Additional supporting information may be found in the online version of this article at the publisher's web-site:

Figure S1: Season of birth. Shows in what quartile of the year dogs in the dataset were born.

Figure S2: Season of test. Shows in what quartile of the year dogs in the dataset were tested.

Figure S3: Scree plot for the principal component analysis.

Table S1: DMA protocol as used by the Swedish working dog club. Describes behaviour reactions for each of the subtest on a 1–5 intensity scale.