Received: 30 August 2024 | Accepted: 1 January 2025

DOI: 10.1111/age.13508

RESEARCH ARTICLE

ANIMAL GENETICS WILEY

Genome-wide study suggests inheritance of personality traits in Toy Poodles and Miniature Dachshunds

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Funding information
Japan Society for the Promotion of Science, Grant/Award Number: 19H04904 and 22H04449

Abstract

Domestic dogs exhibit significant diversity in both morphology and personality. Recent studies focusing on large-breed dogs reported the contribution of genetic factors to personality. However, the genetic influence in small-breed dogs remains unexplored. In the present study, we investigated the personality of two small-breed dogs using a questionnaire and genome-wide single-nucleotide polymorphism data obtained from 301 Toy Poodles and 183 Miniature Dachshunds using the Illumina CanineHD 230K SNP BeadChip. The factor analysis conducted on a questionnaire consisting of 39 items identified seven factors. Among the seven personality factors, 'activeness' in Toy Poodles and 'human-directed sociability' in Miniature Dachshunds had an estimated heritability of 0.425 (SE = 0.311) and 0.514 (SE = 0.355), respectively. In addition, genome-wide association study suggested that two genomic regions possibly affect personality. The dog breeds focused on in this study are most popular in Japan, thus their information is in high demand.

KEYWORDS

behavioral trait, inheritance, Miniature Dachshund, personality, SNP, Toy Poodle

INTRODUCTION

Dogs were the first animals to be domesticated (Ahmad et al., 2020). Currently, humans maintain deep relationships with dogs, not only as working animals but also as friends and family members (Cohen, 2002). In Japan, dogs are the second most common pet after cats (Japan Pet Food Association, 2020), with Toy Poodles and Miniature Dachshunds being the most popular breeds as pets (Anicom Holdings Inc). Both researchers and animal keepers have a key interest in dogs' personalities to ensure a better life with these animals (Ilska et al., 2017).

Previous studies focusing on dogs identified that personality is influenced by both the environment and genetic factors. One study investigated 28 943 Labrador Retrievers and reported on the polygenic effect on personality traits in dogs (Ilska et al., 2017). Studies have reported that polymorphisms in androgen receptors in Akita Inu dogs are associated with aggression (Konno et al., 2011) and single nucleotide polymorphisms (SNPs) are associated with successful training of drug detection dogs, such as German Shepherds and Labrador Retrievers (Matsumoto et al., 2023). Most studies have focused on large-breed dogs, and studies on the behavioral characteristics of small- breed dogs are limited. Therefore, studies on the genetic basis of personality traits in small-breed dogs are required.

In this study, we aimed to explore the genetic basis of the personalities of popular pet dogs. First a questionnaire survey was performed on owners of Toy Poodles and Miniature Dachshunds. We then performed a genomic heritability estimation and genome-wide association analysis to explore the genetic basis of dogs' personalities.

MATERIALS AND METHODS

This study was conducted in accordance with the ethical guidelines of the Wildlife Research Center (Ethical Review Number: WRCH-2021-0002).

Dogs

All dogs used in this study were either purebred Toy Poodles ($n=301$; 140 males and 161 females) or Miniature Dachshunds ($n=183$; 103 males and 78 females; two owners did not provide the sex of their dogs). These two breeds are among the most popular pet dog breeds in Japanese households (Anicom Holdings Inc, 2023). The dogs were raised in Japanese households and registered with Anicom Insurance, Inc. All dogs were aged between 7 and 12 years, with an average age of 10 years.

Questionnaire survey

We conducted a questionnaire survey between 2019 and 2022 to assess the dogs' personalities. Questionnaires were sent to each household by the Anicom Specialty Medical Institute Inc. (Yokohama, Japan), along with a set of swabs for DNA collection. The questionnaire consisted of 39 items regarding the dogs' usual behavior and personality (Table 1) with personality-describing adjectives and their corresponding behavioral definitions, and each item was rated on a 6-point scale ranging from 1 to 6. This questionnaire was a more detailed version of the one previously used to evaluate the characteristics of Akita Inu dogs (Konno et al., 2011). Behaviors toward humans and dogs were independent items in our study. In Konno et al. (2011), they first hypothesized five factors of personality traits and created the questionnaire items based on these factors. They then confirmed that the items were included in the hypothesized factors as expected. See electronic supplementary materials in Konno et al. (2011) for the full questionnaire.

Factor analysis

An exploratory search for the number of factors and factor rotations was conducted across breeds using questionnaire survey data on R software (ver. 4.0.3) (R Core Team, 2023). Factor counts were determined using parallel analysis scree plots, minimum partial correlation means, and the Bayesian information criterion using psych package version 2.3.9 (Revelle, 2023). Oblimin rotation, an oblique rotation, was selected for the rotation of the factor axes, and the maximum likelihood method was used. The validity of each factor was confirmed using Cronbach α using psych package. We determined that Cronbach $\alpha > 0.7$ was valid enough. Factor

TABLE 1 Items of the questionnaire.

No.	Adjective	Defining statement
1	Active	Eager to play, run, and move around as much as possible
2	Easily accustomed (to human)	Adjusts easily to unfamiliar people
3	Easily accustomed (to dogs)	Adjusts easily to unfamiliar dogs
4	Aggressive (to human)	Fights or threatens to fight with people they do not like
5	Aggressive (to dogs)	Fights and threatens dogs they do not like
6	Affectionate	Seeks close contact, such as petting, body contact, etc.
7	Anxious	Shows signs of distress or uneasiness when worried about something
8	Attentive	Pays close attention to what the owner says and does
9	Calm (to human)	Calm and composed in their demeanor, even with strangers
10	Calm (to dogs)	Calm and composed in their demeanor, even with a strange dog
11	Cautious	Avoids risky behavior and be cautious of new things
12	Focused	Able to concentrate on tasks and play, and to hold attention for long periods
14	Curious	Shows strong interest in new things and wants to play with something new
14	Defiant (to human)	Intimidates even owners and family members
15	Defiant (to dogs)	Threatens even known canines
16	Distractible	Attention is easily distracted
17	Dominant (to human)	Acts according to their own wishes and gets angry when others are disturbed
18	Dominant (to dogs)	Acts as they please and gets angry when other dogs mess with them
19	Excitable	Easily agitated, more agitated than other dogs
20	Fearful	Severely frightened or nervous about scary things
21	Friendly (to human)	Can get along with anyone and everyone
22	Friendly (to dogs)	Can get along with anyone, any dogs
23	Gentle (to human)	Responds to others in a calm and kind manner
24	Gentle (to dogs)	Responds to other canines in a calm and gentle manner
25	Impulsive	Unable to control their emotions and does not listen to their owner's commands well
26	Inquisitive	Eager to learn about new things and willing to investigate
27	Inventive	May exhibit new and unexpected behaviors and games
28	Short-tempered (to human)	Lacks patience and easily offends people they do not like

TABLE 1 (Continued)

No.	Adjective	Defining statement
29	Short-tempered (to dog)	Lacks patience and easily offends dogs they do not like
30	Mischievous	Likes to chew, hide things, and make mischief
31	Unhappy	Often moody, with emotional ups and downs
32	Nervous	Vulnerable and sensitive, easily upset by the slightest thing
33	Playful	Strong desire to play and have fun with many things
34	Easily distracted	Easily distracted but loses interest quickly
35	Restless	Difficult to calm down and difficult to make quiet
36	Social (to human)	Seeks to get along with humans
37	Social (to dogs)	Will try to get along with other canines
38	Timid	Easily frightened and unsure in new situations
39	Alert	Cautious and attentive to everything and everyone around them

rotation was performed using the GPA rotation package (ver. 2014.11.1) (Bernaards & Jennrich, 2005) to provide uniqueness to the factors. Each factor was named based on the item with the highest factor loading (Table S1). Items with factor loadings >0.40 were considered significant within each factor. The validity of the questionnaire results as a sample was determined using the Kaiser–Meyer–Olkin function. We determined that Kaiser–Meyer–Olkin function > 0.8 was significant.

The factor scores for each individual were calculated using the Harman method and the 'factor.scores' function. These factor scores were used as characteristics of each individual. The differences between sex of factor scores were tested with Welch' T test.

DNA extraction and genotyping

Buccal swabs were obtained by dog owners by rubbing the inside of the dog's cheek with a sterile swab. The swabs were placed in tubes. They then sent the swabs back with the completed questionnaires. Genomic DNA was extracted from those swabs using the chemagic™ 360 (Perkin Elmer; SCIEX, Waltham, MA, USA) with lysis buffer and Proteinase K (Qiagen, Redwood City, CA USA).

SNPs were genotyped using the Illumina CanineHD 230K SNP BeadChip (Illumina Inc., San Diego, CA, USA) for genome-wide SNP genotyping, following the standard protocols provided by the manufacturer. We used CanFam 3.1 as the genome assembly build. Individuals who had sex-matched SNP data and individual genetic information or questionnaire answers were used in the analysis. Sex determination from SNP information was performed using PLINK v 1.90 (Chang et al., 2015; Purcell et al., 2007) – check-sex option, and F estimates >0.8 were considered males. To control for quality, SNPs with minor allele frequencies <0.01, missing SNP data, or missing 0.05 SNPs overall were excluded. Mitochondrial DNA and SNPs on sex chromosomes were also excluded.

Population genetic analysis

We performed principal component analysis (PCA) to evaluate the population genetic structure in target populations. PCA was performed using --pca option implemented in PLINK v1.90.

Heritability estimation

The genomic heritability for each personality trait was estimated using Genome-wide Complex Trait Analysis (GCTA) version 1.93.2 beta for Windows (Yang et al., 2011). The log-likelihood ratio test was used to estimate genetic variance, residual variance, phenotypic variance, and standard errors. Heritability was estimated based on genome-wide SNP data as a ratio of genetic variance to phenotypic variance. Heritability was tested using the genomic restricted maximum likelihood method implemented in GCTA. Statistical significance was set at 0.05. Those that showed significant genetic effects proceeded to further analysis.

Genome-wide association study

We performed a genome-wide association study (GWAS) for those traits that showed significant genetic effects. We used the same genomic relationship matrix that we used for the heritability estimation. In the genome-wide association analysis, a linear mixed model was fitted using GEMMA software (Zhou & Stephens, 2014). We tested the association between SNP genotypes and personality factor score. To handle the efficiency of the population structure on GWAS, we used a centered relatedness matrix option (-gk 1) in GEMMA as a random effect. To reduce the probability of false positives by multiple testing, we set our significance threshold and suggestive threshold at 0.05 and 1, respectively, per number of SNPs used in the analyses (Friedrich et al., 2019; Ilska et al., 2017). The suggestive levels were set at 6.387e-06 (for Miniature Dachshunds) and 5.997e-06 (for Toy Poodles), and significance levels were set at 3.194e-07 (for Miniature Dachshunds) and 2.999e-07 (for Toy Poodles). The genomic inflation factor (λ) was calculated by dividing the median of the resulting chi-square test statistic of the p-value by the expected median of the chi-square distribution in R. Thereafter, we created Manhattan plots using R package qqman (Turner, 2018).

RESULTS

Factor analysis

Since most factors did not have significant differences between the sexes in factor scores tested using Welch's *t* test (Table S2), the analysis was performed without separating the sexes. Parallel analysis suggested a seven-factor, seven-component structure; the Velicer minimum partial correlation mean achieved a minimum of 0.01 for seven factors and the Bayesian information criterion achieved a minimum of −1686.3 for seven factors. Subsequently, the validity of these factors was evaluated as follows.

The mean measures of sampling adequacy was 0.86, with a minimum value of 0.68, which was sufficient to withstand factor analysis. Manipulations were performed on R using the psych package (ver. 2.1.6) (Revelle, 2023). All personality factor scores were normally distributed (Figure 1). The Cronbach α of each factor was >0.7 (Table 2). We treated those personality factor scores as phonotypes in the following analysis.

Population structure

In total, 211 Toy Poodles and 148 Dachshunds, with 166 735 and 156 557 SNPs, respectively, remained after quality control. There was no clear population structure based on PCA plots (Figure 2).

Genomic heritability

The heritability of the seven personality traits was based on genomic data (Table 3). We found suggestive but high heritability for one trait in Toy Poodles (activeness, $V_G/V_P=0.425$, SE = 0.310, $p=0.080$) and one trait in Miniature Dachshunds (human-directed sociability [HDS], $V_G/V_P=0.514$, SE = 0.355 $p=0.078$).

GWAS

We performed a GWAS for traits showing significance genetic effects (Figure 3). Activeness was subjected to GWAS for Toy Poodles, with a genomic inflation factor (λ) of 1.040. HDS was subjected to GWAS for Miniature Dachshunds, with a genomic inflation factor (λ) of 1.01.

We found no SNPs that exceeded the significance level; however, five SNPs were detected as candidate SNPs with suggestive level association. Four SNPs may be associated with HDS in Miniature Dachshunds (Table 4). These SNPs are located in the intronic region of the Astrotactin 1 gene (*ASTN1*), and the intronic region of RAS P21 Protein Activator 3 (*RASA3*) and ENSCAFG00000045469. The other SNP was not located in the protein coding region nor in the transcript.

The SNP potentially associated with activeness in Toy Poodles (Table 4) is located in the exon region of coiled-coil domain containing 198 gene (*CCDC198*).

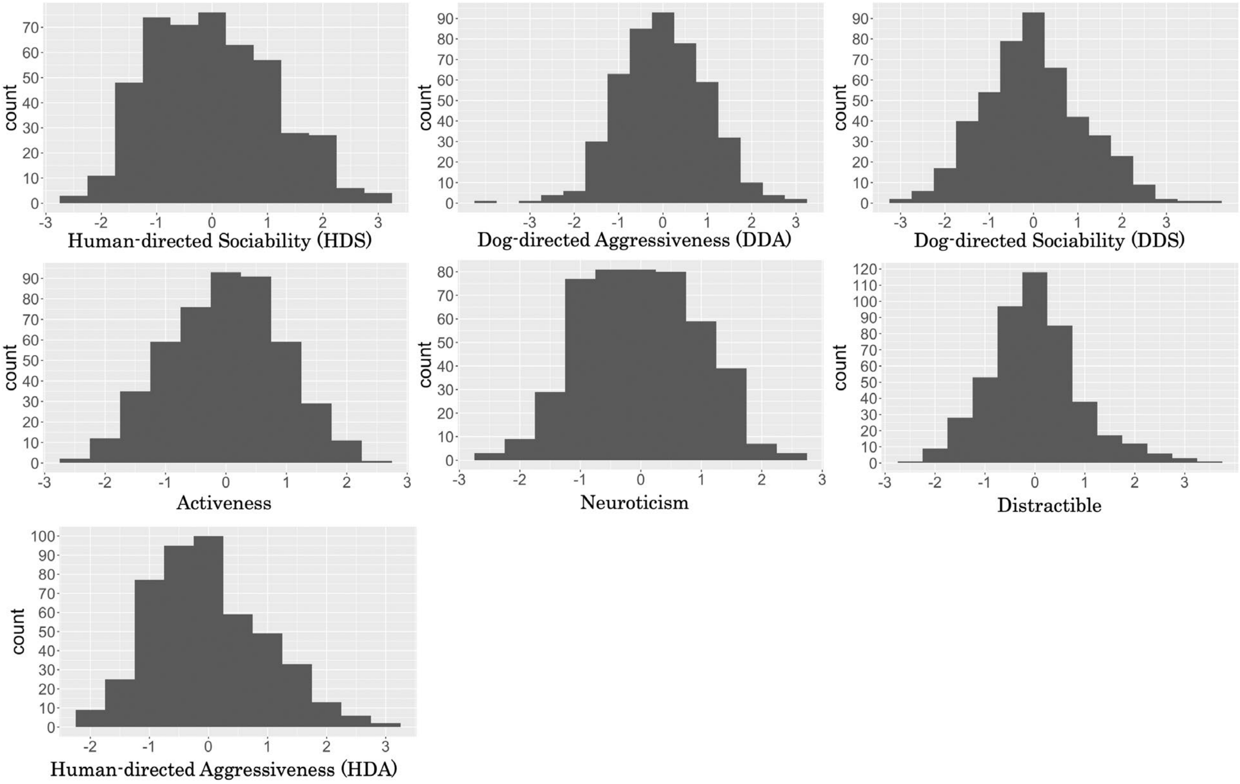
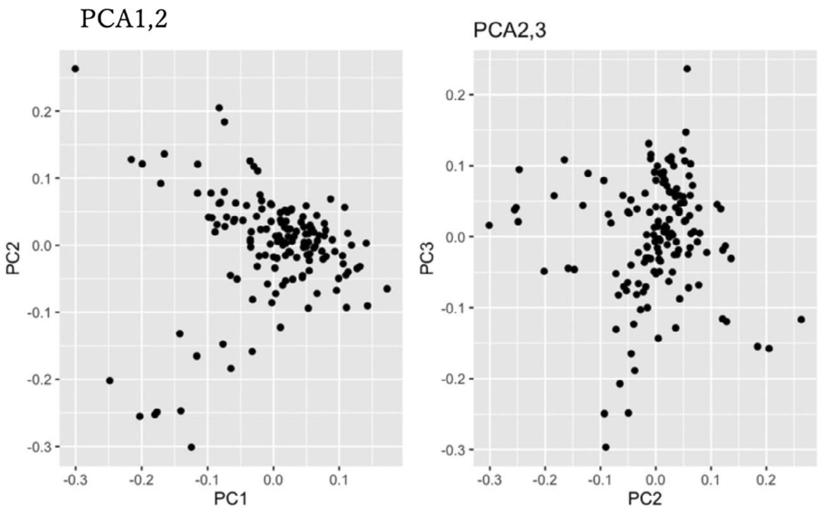


FIGURE 1 Distribution of scores for each personality factor.

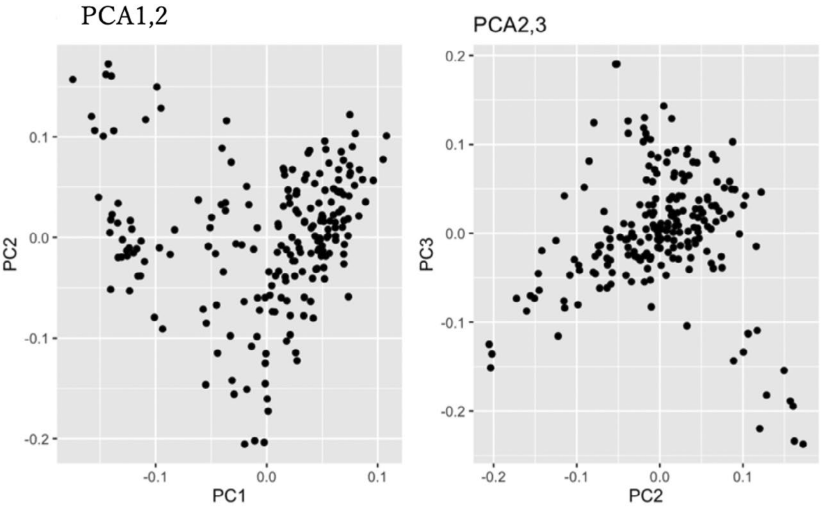
TABLE 2 Cronbach α values of each factor.

Factor	Trait	Raw α	Std. α
1	HDS (human-directed sociability)	0.8987909	0.8986773
2	DDA (dog-directed aggressiveness)	0.8592162	0.8617206
3	DDS (dog-directed sociability)	0.9166767	0.9169873
4	Activeness	0.7961751	0.7955129
5	Neuroticism	0.7833847	0.7794037
6	Distractible	0.7038495	0.7030136
7	HDA (human-directed aggressiveness)	0.7994167	0.8028537

FIGURE 2 Principal component analysis of SNPs of two breeds, Miniature Dachshunds and Toy Poodles.



Toy Poodles



DISCUSSION

Studies focusing on small-breed dogs' personalities are limited. In this study, to assess the genetic effect on personality traits, we measured dogs' personality traits quantitatively using a questionnaire survey, estimated heritability and performed a GWAS. This study showed that two personality traits, activeness in Toy Poodles and HDS in Miniature Dachshunds, are affected by genetic factors.

We estimated the heritability of personality traits and found high heritability of activeness in Toy Poodles and HDS in Miniature Dachshunds (Table 3). Those estimated heritability values indicate the presence of a genetic effect on personality in both breeds. These estimated heritability values were higher than those estimated in previous studies (Strandberg et al., 2005; van der Waaij et al., 2008). In the study by Strandberg et al. (2005), the heritability of playfulness, curiosity/fearlessness, and aggressiveness in German Shepherds was <0.4, and van der Waaij et al. (2008) found that the heritability of behavioral test scores in the Labrador Retriever and German Shepherds was <0.4, except for gun shyness in the Labrador Retriever. Both previous studies estimated pedigree-based heritability, and our current study estimated the heritability based on genome-wide SNPs. Moreover, the SNP-based heritability estimation of HDS in Miniature Dachshunds and activeness in Toy Poodles in our study was much higher than that of the Canine Behavioral Assessment and Research Questionnaire (C-BARQ) scores in German Shepherds (Friedrich et al., 2019). Toy Poodles and Dachshunds are thought to be more recently bred than Labrador Retrievers and German Shepard Dogs (Wayne & vonHoldt, 2012) and are considered to be more homogeneous in their populations. This may have resulted in those high heritabilities. Moreover, differences in the methods used to estimate heritability and breed type (large or small), may be associated with variations in heritability score. Our questionnaire includes some questions that are similar to those in C-BARQ. A factor (dog-directed aggressiveness) is comparable to factors in C-BARQ.

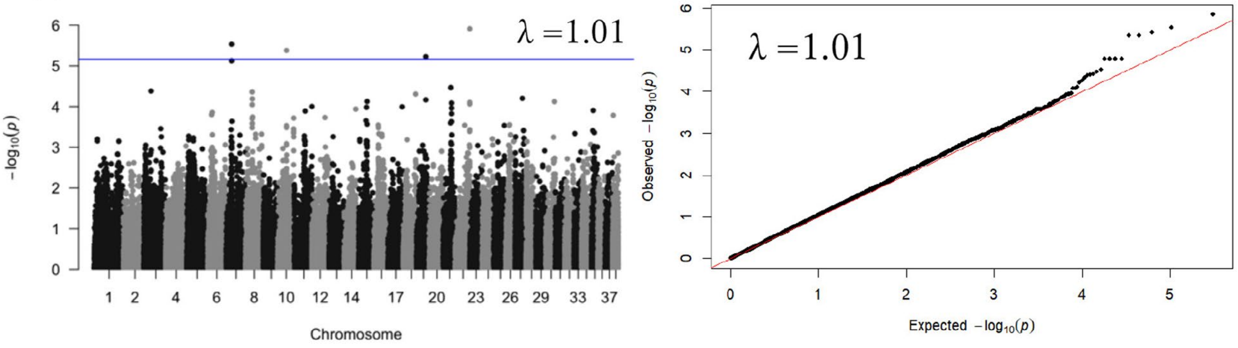
We found five SNPs that were not significant but may be related to personality traits (Table 4). Four SNPs were suggested to be corelated to HDS in Miniature Dachshunds. One of them were in the intronic region

TABLE 3 Heritability (V_G/V_P) in each trait and breed.

Breed	Trait	V_G/V_P	SE	*p*
MD	HDS	0.51351	0.35508	0.078
MD	DDA	0.0646	0.37991	0.480
MD	DDS	1E-06	0.36323	0.500
MD	Activeness	1E-06	0.36268	0.500
MD	Neuroticism	1E-06	0.40568	0.500
MD	Distractible	0.26318	0.32519	0.157
MD	HDA	0.08012	0.29245	0.373
TP	HDS	1E-06	0.29093	0.500
TP	DDA	1E-06	0.32841	0.500
TP	DDS	1E-06	0.25062	0.500
TP	Activeness	0.42514	0.3107	0.080
TP	Neuroticism	1E-06	0.29926	0.500
TP	Distractible	1E-06	0.30759	0.500
TP	HDA	1E-06	0.28562	0.500

Abbreviations: DDA, dog-directed aggressiveness; DDS, dog-directed sociability; HDA, human-directed aggressiveness; HDS, human-directed sociability; MD, Miniature Dachshunds; TP, Toy Poodles.

(a) Miniature Dachshunds' HDS



(b) Toy Poodles' Activeness

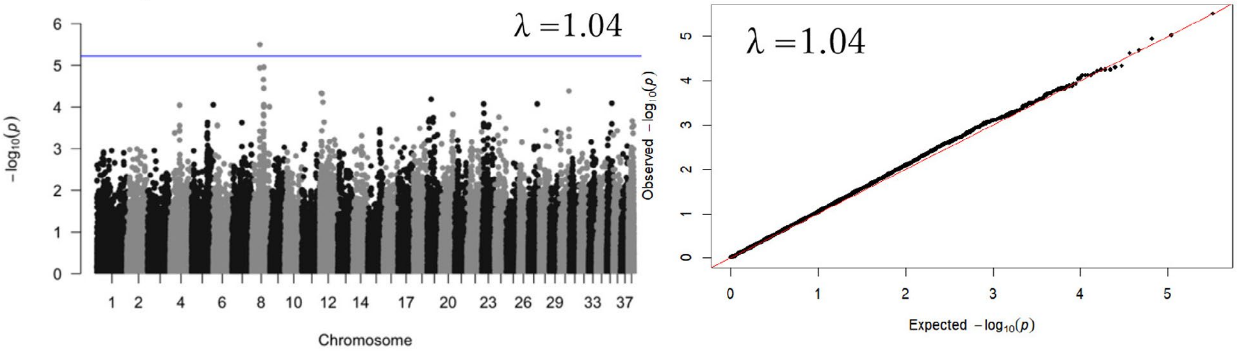


FIGURE 3 Manhattan plots fitted using linear mixed model and QQ plots. (a) Miniature Dachshunds' human-directed sociability, (b) Toy Poodles' activeness. The blue lines on Manhattan plots shows the suggestive level.

TABLE 4 SNPs whose *p*-values was beyond the suggestive level and genes overlapped with the SNPs.

Breed	Trait	CHR	SNP	BP	Allele 1	Allele 0	Allele frequency	SE	*p*-Value	Adjusted *p*-value	Gene ID	Exon/intron
MD	HDS	7	BICF2P1123710	2.3E+07	G	A	0.459	−206.32	2.94E-06	0.4526503	ENSCAFG00000014179 (*ASTN1*)	Intron 16–17 (ASTN1-202)/Intron 15–16 (ASTN1-202)/ Intron16-17 (ASTN1-203)
MD	HDS	10	BICF2P399349	3.7E+07	G	A	0.331	−207.3	4.17E-06	0.642896	–	–
MD	HDS	19	BICF2S23122969	3.9E+07	A	G	0.231	−207.75	5.95E-06	0.91717	ENSCAFG00000045469	–
MD	HDS	22	BICF2P964740	6.1E+07	A	C	0.33	−205.04	1.22E-06	0.1887248	ENSCAFG00000000645 (*RASA3*)	Intron 11–12 (RASA3-202)/Intron 10–11 (RASA3-201)
TP	Activeness	8	chr8_32999077	3.3E+07	A	G	0.389	−268.37	3.16E-06	0.5179766	ENSCAFG00000015253 (*CCDC198*)	ENSCAFE00000166092

Note: The adjusted *p*-values were calculated with number of SNPs (166 735 SNPs of Toy Poodle and 156 557 SNPs of Dachshund) using Bonferroni methods.

Abbreviations: CHR, chromosome; MD, Miniature Dachshunds; TP, Toy Poodles.

of *ASTN1*. Astrotactin guides neuroblast migration along glia in developing brain cortical regions (Fink et al., 1997). In humans, variations within *ASTN1* are reportedly related to alcohol dependence (Hill et al., 2012) and schizophrenia (Kähler et al., 2008). These SNPs may affect behavior, including HDS. One of those was in the intronic region of *RASA3*. *RASA3* is a GTPase activating protein of the GAP1 subfamily, which targets Ras and Rap1. *RASA3* mRNA is highly expressed in the brain, mainly in neuronal cells (Schurmans et al., 2015). This could mean that *RASA3* is related to HDS via memory of dogs.

One SNP, located in the exon of the *CCDC198* gene, was found to be associated with activeness in Toy Poodles. *CCDC198* evolves at an exceptional rate in birds and mammals, as well as *1700011H14Rik*/*C14orf105* (Petersen et al., 2023). They are membrane-associated proteins enriched in the kidney, pancreas, liver, and fallopian tubes in humans. Knockout models of these genes show significant effects as compared to the same background wild type controls in metabolic cage experiments, including differences in body mass indexes (Petersen et al., 2023). This may be due to the efficiency of energy metabolism affecting activeness.

In a previous study, *TH*, *CLINT1*, and *CADPS2* were associated with personality traits in Labrador Retrievers (Ilska et al., 2017). These genes may play roles in the brain and may be associated with developmental disorders in humans. Unannotated protein-coding genes related to RNA binding and structural constitution of ribosomes, *AQP4*, *HIVEP2*, *AIG2*, *KCNAB*, *AMDHD1*, *HAL*, *BRWD1*, *B3GALT5*, and *ARNT*, have been reported with GWAS and regional heritability mapping in German Shepherds (Friedrich et al., 2019). These genes are related to body size, developmental disorders, voltage-gated potassium channels, or the central nervous system. Two possible explanations for the lack of agreement in SNPs are stronger effects within varieties and differences in phenotypic composition. Friedrich et al. (2019) did not obtain the same results as reported by Ilska et al. (2017). The genetic basis of behavior and personality may be also affected the breeds. Our results showed different results between the two varieties. While the first two studies used the C-BARQ, the present study used a questionnaire in Japanese, and the factors extracted from the questionnaire were used as traits. Moreover, no SNPs suggested in this study overlap with SNPs found or suggested to be associated with the success of drug detection in German Shepherds and Labrador Retrievers (Matsumoto et al., 2023). That study was conducted on a different breed than ours, and it is also a well-trained group, which may differ in nature from the pet dogs. Larger samples sizes are preferred for estimation of heritability and/or GWAS; thus, further research is needed in larger cohorts, such as 500 dogs or more (Matsumoto et al., 2023).

This study revealed genetic effects on activeness and HDS in small-breed dogs. Sociability is a major difference between dogs and wolves and can be an important trait for domestication (Bentosela et al., 2016; vonHoldt et al., 2017). In this questionnaire, the questions related to activeness included those associated with playfulness and mischievousness. Playfulness is strongly influenced by dog breeds (Svarberg & Forkman, 2002). In addition, behaviors show large breed differences among dogs (Asp et al., 2015), which would explain why our results differed among the varieties. The effectiveness of the genetic effect on these behaviors may contribute to behavioral modification and training in small-breed dogs.

AUTHOR CONTRIBUTIONS

Chika Zemmoro: Data curation; methodology; visualization; formal analysis; writing – original draft. **Yuki Matsumoto:** Data curation; formal analysis; funding acquisition; investigation; methodology; resources; supervision; writing – review and editing. **Minori Arahori:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; supervision; writing – review and editing. **Miho Inoue-Murayama:** Conceptualization; funding acquisition; project administration; writing – review and editing.

ACKNOWLEDGEMENTS

This study was financially supported by grants from KAKENHI, Nos. 19H04904 and 22H04449 to M.I.-M and Research Foundation of Anicom Insurance Inc. We would like to thank Dr. Akitsugu Konno for sharing the questionnaire. We would like to thank all dogs and their owners who participated in this study. We would like to thank all members from the Wildlife Research Center and Anicom Specialty Medical Institute Inc. who gave us advice and help. We would like to thank Editage and Annegret Moto Naito Liederbach for English revision.

FUNDING INFORMATION

KAKENHI Nos. 19H04904 and 22H04449 to M.I.-M.

CONFLICT OF INTEREST STATEMENT

We have no conflicts of interest.

DATA AVAILABILITY STATEMENT

DDBJ database (https://www.ddbj.nig.ac.jp/index-e.html), GEA Experimental Accession Number: E-GEAD-828.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Zemmoto, C., Matsumoto, Y., Arahori, M. & Inoue-Murayama, M. (2025) Genome-wide study suggests inheritance of personality traits in Toy Poodles and Miniature Dachshunds. *Animal Genetics*, 56, e13508. Available from: https://doi.org/10.1111/age.13508