

Behavioral Genetics in Companion Animals: Current Insights and Future Directions

Wei Liu, Jia Xuan ✉

Institute of Life Science, Jiyang College of Zhejiang A&F University, Zhuji, 311800, Zhejiang, China

✉ Corresponding author: jia.xuan@jicaf.org

Animal Molecular Breeding, 2024, Vol.14, No.4 doi: [10.5376/amb.2024.14.0030](https://doi.org/10.5376/amb.2024.14.0030)

Received: 03 Jul., 2024

Accepted: 13 Aug., 2024

Published: 28 Aug., 2024

Copyright © 2024 Liu and Xuan, This is an open access article published under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

Preferred citation for this article:

Liu W., and Xuan J., 2024, Behavioral genetics in companion animals: current insights and future directions, Animal Molecular Breeding, 14(4): 288-296 (doi: [10.5376/amb.2024.14.0030](https://doi.org/10.5376/amb.2024.14.0030))

Abstract This study explores the latest advances in behavioral genetics, emphasizing the identification of key genetic markers, the role of gene environment interactions, and the impact of variety specific characteristics on behavior. It includes strengthening training programs, identifying genetic diseases associated with behavioral problems, and supporting selective breeding to improve temperament and other practical applications. The case study of working dogs demonstrates that genetic and environmental factors are interdependent in optimizing task performance, emphasizing the potential of future technologies such as CRISPR and artificial intelligence to expand research to underserved species and personalized behavior management methods. This study aims to emphasize the transformative role of behavioral genetics in improving companion animal welfare and training methods.

Keywords Behavioral genetics; Companion animals; Gene-environment interactions; Animal welfare; Selective breeding

1 Introduction

Behavioral genetics in companion animals, particularly dogs, has been a significant area of study due to their close relationship with humans and their diverse behavioral traits. The field examines how genetic variations influence behaviors, utilizing advancements in genomic technologies to explore these connections. Dogs, with their unique evolutionary history and widespread presence, serve as a powerful model for understanding the genetic basis of behavior. Studies have shown that while certain behavioral traits are heritable, the genetic architecture is often complex and polygenic, involving multiple genes with small effects (Morrill et al., 2022; Lord et al., 2024). This complexity is compounded by the influence of environmental factors, making the study of behavioral genetics in companion animals a challenging yet promising field (Toth and Rehan, 2019).

Understanding behavioral traits in companion animals is crucial for several reasons. It aids in improving animal welfare by identifying genetic predispositions to certain behaviors, which can inform breeding practices and behavioral interventions. For instance, recognizing the genetic basis of traits like aggressiveness or sociability can help in selecting suitable pets for different environments and purposes (Inoue-Murayama, 2012; Grandin, 2013). Moreover, insights gained from studying companion animals can have broader implications, including applications in human behavioral genetics, as many genetic mechanisms are conserved across species (Plassais et al., 2019). This knowledge also enhances our understanding of the domestication process and the evolutionary adaptations that have shaped the behaviors of companion animals (Zhang et al., 2020).

This study integrates current knowledge on the genetic basis of companion animal behavior, with a focus on dogs, and identifies future research directions, covering the exploration of genetic diversity within and between breeds, understanding the polygenic nature of behavioral characteristics, and examining the interactions between genetic and environmental factors. It extends to practical applications, such as improving breeding strategies and strengthening human animal relationships through a better understanding of behavioral genetics. This study aims to provide a comprehensive overview of the field by integrating the results of various studies and highlighting areas that require further research to fully realize the potential of companion animal behavioral genetics.

2 Behavioral Genetics in Companion Animals

2.1 Definition and scope of behavioral genetics

Behavioral genetics is the study of how genetic factors influence behavioral traits in animals, including companion animals such as dogs and cats. This field examines the heritable components of behavior and how these genetic factors interact with environmental influences to shape individual behaviors. The scope of behavioral genetics extends from understanding basic genetic mechanisms to applying this knowledge in practical settings, such as improving animal welfare and breeding programs. The discipline has evolved significantly, with advances in genomic technologies enabling more detailed investigations into the genetic basis of behavior (Per and Dominic, 2013; Krüger et al., 2017).

2.2 Key genetic markers associated with companion animal behavior

Research in behavioral genetics has identified several genetic markers associated with behavioral traits in companion animals. For instance, genome-wide association studies (GWAS) have revealed specific loci linked to behaviors such as sociability and biddability in dogs (Ilska et al., 2017). These studies highlight the polygenic nature of behavioral traits, where multiple genes contribute to the observed behaviors. Additionally, certain genes have been found to influence behaviors across different species, suggesting conserved genetic pathways that govern behavior (Alvarenga et al., 2021). Despite these findings, the genetic basis of behavior remains complex, with many traits influenced by both genetic and environmental factors (Bubac et al., 2020).

2.3 Advances in genomic tools for behavioral studies

The field of behavioral genetics has greatly benefited from advances in genomic tools, which have enhanced the ability to study the genetic basis of behavior in companion animals. Techniques such as whole genome sequencing and GWAS have become more accessible, allowing researchers to identify genetic variants associated with specific behaviors (Plassais et al., 2019). These tools have enabled the exploration of genetic diversity within and between breeds, providing insights into how selection pressures have shaped behavioral traits (Morrill et al., 2022). Furthermore, integrating genomic data with behavioral assessments has opened new avenues for understanding the complex interactions between genes and the environment, paving the way for more targeted breeding and conservation strategies (Bengston et al., 2018).

3 Current Insights into Behavioral Genetics

3.1 Genetic basis of aggression and temperament in dogs and cats

The genetic basis of aggression and temperament in dogs is a complex interplay of multiple genetic factors. Studies have identified several genetic loci associated with behavioral traits such as fear, anxiety, and aggression. For instance, genome-wide association studies (GWAS) have revealed that genes like *MSRB3* and *CHLI* are linked to fear-related behaviors in dogs (Shan et al., 2021). Additionally, the *IGF1* and *HMG2* loci have been associated with aggression and anxiety, suggesting a genetic overlap between behavior and morphology (Zapata et al., 2016). These findings highlight the polygenic nature of these traits, where multiple genes contribute small effects to the overall behavior (Ilska et al., 2017).

3.2 Influence of gene-environment interactions on behavioral outcomes

Gene-environment interactions play a significant role in shaping behavioral outcomes in companion animals (Lin, 2024). Environmental factors such as upbringing, training, and socialization can significantly influence the expression of genetic predispositions. For example, DNA methylation, an epigenetic mechanism, has been shown to correlate with behaviors like energy levels and fear responses in dogs, indicating that environmental factors can modify genetic expression (Figure 1) (Sanders et al., 2022). This interaction underscores the importance of considering both genetic and environmental influences when assessing animal behavior (Hecht et al., 2021).

3.3 Role of breed-specific traits in behavioral patterns

Breed-specific traits have traditionally been thought to predict certain behavioral patterns in dogs. However, recent research challenges this notion, showing that breed explains only a small percentage of behavioral variation. For example, a study of Morrill et al. (2022) found that breed accounts for just 9% of behavioral differences, suggesting that individual variation is more significant than breed stereotypes. While certain traits like trainability

may have higher heritability within breeds, behaviors such as aggression and fearfulness are influenced by a broader range of genetic and environmental factors (Peřková et al., 2024). This indicates that while breed can provide some insights into potential behavioral tendencies, it should not be the sole factor in predicting an individual animal's behavior.

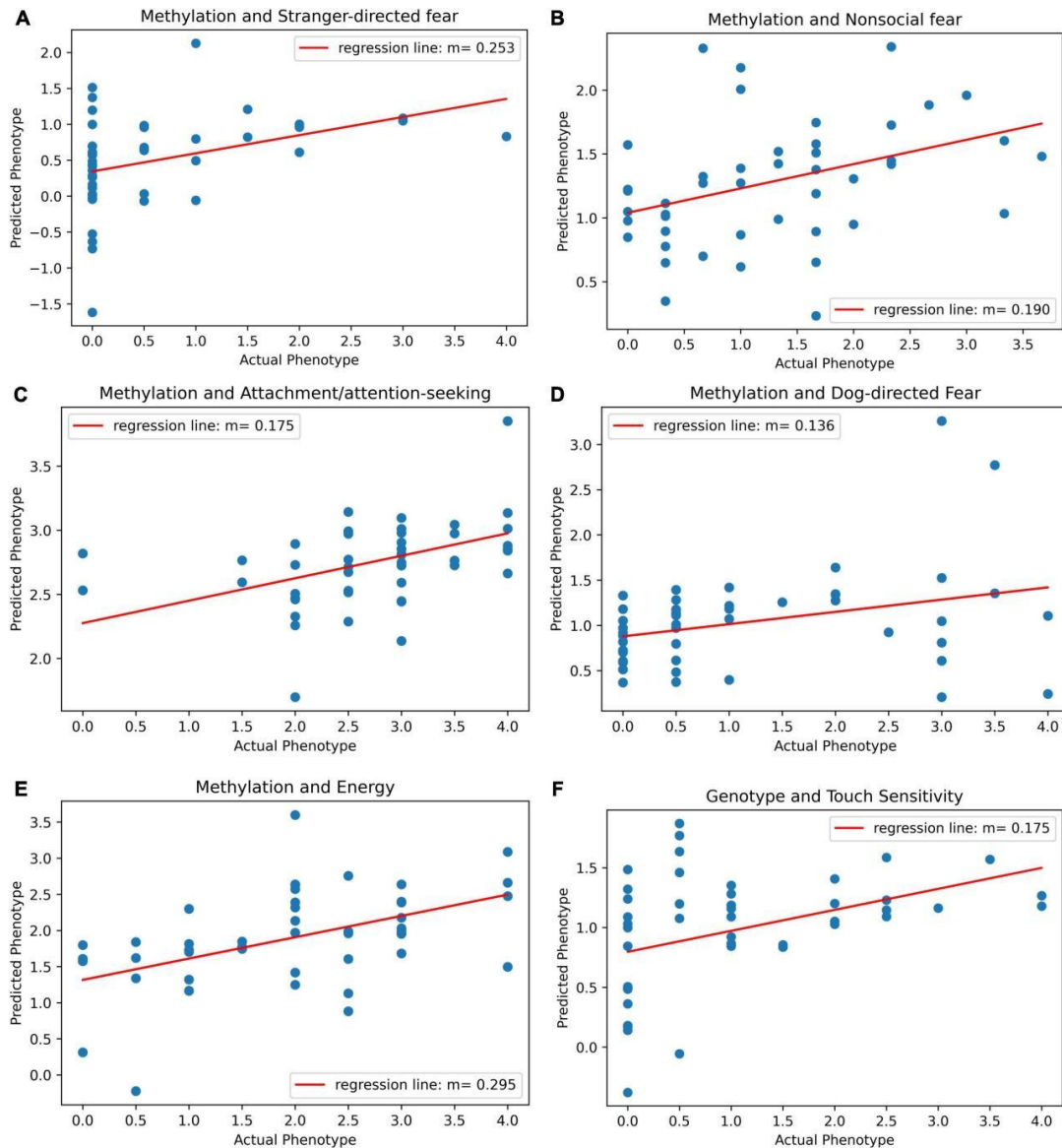


Figure 1 (A) Scatter plot of predicted vs. actual phenotype for stranger-directed fear. Actual stranger-directed fear values were recorded by the C-BARQ survey. Predicted phenotype scores were generated by PLS regression on methylation values. The plot specifies the slope of the best-fit line through the plotted points. (B) Scatter plot of predicted vs. actual phenotype for non-social fear. Actual non-social fear values were recorded by the C-BARQ survey. Predicted phenotype scores were generated by PLS regression on methylation values. The plot specifies the slope of the best-fit line through the plotted points. (C) Scatter plot of predicted vs. actual phenotype for attachment/attention-seeking. Actual attachment/attention-seeking values were recorded by the C-BARQ survey. Predicted phenotype scores were generated by PLS regression on methylation values. The plot specifies the slope of the best-fit line through the plotted points. (D) Scatter plot of predicted vs. actual phenotype for dog-directed fear. Actual dog-directed fear values were recorded by the C-BARQ survey. Predicted phenotype scores were generated by PLS regression on methylation values. The plot specifies the slope of the best-fit line through the plotted points. (E) Scatter plot of predicted vs. actual phenotype for energy. Actual energy values were recorded by the C-BARQ survey. Predicted phenotype scores were generated by PLS regression on methylation values. The plot specifies the slope of the best-fit line through the plotted points. (F) Scatter plot of predicted vs. actual phenotype for touch sensitivity. Actual touch sensitivity values were recorded by the C-BARQ survey. Predicted phenotype scores were generated by PLS regression on genotype values. The plot specifies the slope of the best-fit line through the plotted points (Adopted from Sanders et al., 2022)

4 Applications of Behavioral Genetics in Companion Animal Welfare

4.1 Enhancing training programs through genetic insights

Behavioral genetics offers significant potential to enhance training programs for companion animals by providing insights into the genetic basis of behavior. Understanding the genetic predispositions of animals can help tailor training methods to suit individual needs, thereby improving the effectiveness of these programs. For instance, certain breeds of dogs have been shown to possess genetic traits that make them more amenable to specific types of training, such as herding or guarding behaviors (Per, 2013). By identifying these genetic markers, trainers can develop more targeted approaches that align with the natural inclinations of the animal, reducing stress and increasing the likelihood of successful training outcomes. Additionally, genetic insights can help identify animals that may require alternative training strategies due to behavioral challenges linked to their genetic makeup, such as anxiety or aggression (Broom, 2015). This personalized approach not only enhances the welfare of the animals by promoting positive behavioral outcomes but also strengthens the bond between pets and their owners.

4.2 Identifying genetic disorders linked to behavioral issues

Identifying genetic disorders that are linked to behavioral issues is a crucial application of behavioral genetics in improving companion animal welfare. Many behavioral problems in pets, such as anxiety, aggression, or compulsive behaviors, can be traced back to genetic anomalies. For example, certain breeds of dogs are predisposed to neurological issues due to over-selection for specific traits, which can manifest as behavioral disorders (Grandin and Deesing, 2014). By pinpointing these genetic disorders, veterinarians and animal behaviorists can develop more effective treatment plans that address the root cause of the behavior rather than just the symptoms. This approach not only improves the quality of life for the animals but also helps in managing expectations and responsibilities for pet owners. Furthermore, understanding these genetic links can guide breeders in making informed decisions to avoid perpetuating these disorders in future generations, thereby enhancing the overall welfare of companion animals (Jensen, 2018).

4.3 Supporting selective breeding for improved temperament

Selective breeding for improved temperament is another vital application of behavioral genetics that can significantly enhance companion animal welfare (Zhang, 2024). By focusing on genetic traits associated with desirable behaviors, such as sociability, calmness, and adaptability, breeders can produce animals that are better suited to living in human environments (Rydhmer and Canario, 2014). This practice not only reduces the incidence of behavioral problems but also ensures that animals are more likely to thrive in various household settings. Responsible breeding practices that prioritize genetic diversity and select for positive behavioral traits can help mitigate the risks associated with inherited defects and behavioral disorders (Sonntag and Overall, 2014). Moreover, by using genetic insights to inform breeding decisions, breeders can contribute to the development of companion animals that are not only physically healthy but also possess temperaments that enhance their welfare and the well-being of their human companions. This approach aligns with the growing demand for pets that can seamlessly integrate into modern lifestyles, ultimately promoting a harmonious coexistence between humans and their animal companions.

5 Case Study: Behavioral Genetics in Working Dogs

5.1 Genetic traits linked to trainability and task performance

The genetic basis of trainability and task performance in working dogs is a significant area of interest, as these traits are crucial for their roles in various service and working capacities. Research has identified specific genetic variants that influence these behavioral traits. For instance, in Belgian Malinois dogs, variations in the TAC1 gene have been linked to differences in trainability and excitability levels. Two single nucleotide polymorphisms (SNPs) in the TAC1 promoter region were found to affect transcription factor binding, thereby influencing these behavioral traits (Table 1) (Fallahi et al., 2024). Similarly, genome-wide association studies (GWAS) have identified several genes associated with trainability and temperament, such as the ACSS3 gene, which is linked to temperament traits in dogs (Shan et al., 2021). These findings highlight the polygenic nature of behavioral traits, where multiple genes contribute to the overall phenotype, making it essential to consider a broad genetic perspective when assessing trainability in working dogs.

Table 1 Association between the TAC1 SNP genotypes and desired behaviours in Belgian Malinois dogs (Adopted from Fallahi et al., 2024)

SNP	Least square mean±SE						
	Genotype	Excitability *	Aggression	Fear	Separation-related behaviour	Attention	Trainability*
c.-162G>C	GG	10.04±1.18	21.64±3.97	8.85±2.06	8.16±1.58	14.28±1.41	18.02±0.92 B
	GC	6.59±1.80	27.70±6.27	6.55±3.25	8.34±2.50	12.64±2.24	21.10±1.49 A
	CC	10.31±1.65	23.72±5.58	10.96±2.85	6.43±2.18	14.35±1.98	20.28±1.34 AB
c.-89C>T	CC	10.24±0.79 A	21.88±2.75	9.38±1.43	7.60±1.09	14.20±0.97	18.97±0.71
	CT	6.37±1.48 B	28.25±5.29	5.94±2.75	9.24±2.12	12.50±1.88	20.47±1.37
c.* 33T>A	TT	8.90±2.01	26.08±6.74	10.90±3.47	5.89±2.64	14.40±2.40	20.46±1.62
	TA	8.63±1.21	25.93±4.07	8.85±2.12	8.40±1.62	13.76±1.46	18.81±0.98
	AA	9.42±1.32	21.05±4.41	6.61±2.26	8.64±1.75	13.12±1.57	20.13±1.06

Note: Fear=fear and anxiety; attention=attachment and attention-seeking. * Values with different uppercase superscripts in the same column for each SNP are significantly different ($p < 0.05$). Bold values are significant in the same column (Adopted from Fallahi et al., 2024)

5.2 Environmental factors shaping working dog behavior

While genetic factors play a crucial role in shaping the behavior of working dogs, environmental influences are equally significant. The interaction between genes and the environment can significantly impact behavioral outcomes. For example, the presence of children in a household has been associated with increased anxiety traits in dogs, while the presence of other animals can influence behaviors such as coprophagia (Zapata et al., 2020). Additionally, the training environment and the methods used can affect the expression of genetic predispositions. Dogs that are part of genomic selection programs, such as those used for guide dogs, show that environmental stimuli and training regimens can enhance or suppress certain behavioral traits. Moreover, DNA methylation, an epigenetic mechanism, has been shown to correlate with behavioral traits like energy and fear, indicating that environmental factors can lead to epigenetic changes that influence behavior (Sanders et al., 2022). These insights underscore the importance of considering both genetic and environmental factors in the development and training of working dogs.

5.3 Implications for breeding programs and training strategies

The integration of genetic insights into breeding programs and training strategies for working dogs holds significant potential for enhancing their effectiveness and well-being. Understanding the genetic underpinnings of traits such as trainability and temperament can inform selective breeding practices aimed at enhancing desirable traits while minimizing behavioral issues. For instance, genomic selection approaches, such as single-step GBLUP, have been shown to improve the accuracy of breeding value predictions, thereby aiding in the selection of dogs with optimal genetic profiles for specific tasks (Riser et al., 2023). Additionally, recognizing the role of environmental factors and epigenetic influences can lead to more tailored training strategies that accommodate individual genetic predispositions. This holistic approach can optimize the performance and adaptability of working dogs, ensuring they meet the demands of their roles while maintaining their welfare. By combining genetic and environmental considerations, breeding and training programs can be more effective in producing dogs that excel in their working capacities (Turcsán et al., 2011).

6 Challenges in Behavioral Genetics Research

6.1 Ethical considerations in genetic studies of behavior

Ethical considerations in behavioral genetics research are paramount, particularly when it involves companion animals like dogs. The use of genomic technologies, such as CRISPR/Cas9, raises significant ethical concerns, especially regarding germline modifications that cannot be ethically implemented in wild or natural settings (Walton et al., 2020). The potential for altering an animal's genetic makeup to study behavior must be carefully weighed against the welfare of the animals involved. Additionally, the implications of such research on animal breeding practices and the potential for misuse in creating "designer pets" necessitate strict ethical guidelines. The integration of ethical considerations is crucial to ensure that the research does not inadvertently harm the animals

or lead to unintended consequences in their natural behaviors. Furthermore, the transparency of research methodologies and the informed consent of pet owners participating in studies are essential to uphold ethical standards.

6.2 Limitations in current genetic mapping techniques

Current genetic mapping techniques, such as genome-wide association studies (GWAS) and quantitative trait locus (QTL) mapping, face several limitations in behavioral genetics research. These methods often require large sample sizes to detect significant associations between genetic markers and behavioral traits, which can be logistically challenging to obtain. Additionally, the polygenic nature of behavioral traits means that individual genomic regions typically have small effects, complicating the identification of specific genes responsible for behavior. The complexity of behavior, influenced by both genetic and environmental factors, further complicates the mapping process, as many studies fail to replicate findings across different populations or species (Bubac et al., 2020). Moreover, the focus on modern breeds in canine studies limits the genetic diversity explored, potentially overlooking important genetic variations present in mixed-breed or non-breed-specific populations. These limitations highlight the need for more comprehensive and integrative approaches that combine genetic data with environmental and phenotypic information.

6.3 Challenges in integrating genomics with behavioral science

Integrating genomics with behavioral science presents several challenges, primarily due to the complex interplay between genes and the environment in shaping behavior. One major challenge is the historical divide between biological and psychological approaches to studying behavior, which can impede interdisciplinary collaboration. Additionally, the ecological validity of laboratory-based genomic studies is often questioned, as they may not accurately reflect the natural environments in which behaviors occur. This discrepancy can lead to incomplete or inaccurate assessments of gene-behavior relationships. Furthermore, the integration of genomic data with behavioral phenotypes requires sophisticated analytical tools and methodologies to account for the multifactorial nature of behavior (Kent et al., 2019). The need for longitudinal studies that track behavioral changes over time and across different environmental contexts is also critical to understanding the dynamic nature of gene-environment interactions. Addressing these challenges requires a concerted effort to bridge disciplinary gaps and develop innovative research frameworks that incorporate both genomic and behavioral data.

7 Future Directions in Behavioral Genetics

7.1 Role of emerging technologies like CRISPR and AI in behavioral studies

Emerging technologies such as CRISPR and artificial intelligence (AI) hold significant promise for advancing behavioral genetics in companion animals. CRISPR technology allows for precise genetic modifications, which can be used to investigate the causal relationships between specific genes and behavioral traits. This could lead to breakthroughs in understanding complex behaviors by enabling targeted gene editing to observe resultant behavioral changes. AI, on the other hand, can process large datasets from genomic studies and behavioral assessments, identifying patterns and correlations that might be missed by traditional analysis methods. AI algorithms can enhance the predictive accuracy of genetic influences on behavior by integrating diverse data sources, including genomic, environmental, and phenotypic data (York, 2018).

7.2 Expanding research into understudied companion animal species

While dogs have been extensively studied in behavioral genetics, there is a need to expand research to other companion animals such as cats, birds, and small mammals. These species have unique behavioral traits and genetic backgrounds that can provide new insights into the genetic basis of behavior. Expanding research to these underrepresented species can help in understanding species-specific behaviors and the evolutionary aspects of domestication. Additionally, studying a broader range of species can improve our understanding of the genetic diversity and adaptability of companion animals, which is crucial for conservation and welfare efforts (Alvarenga et al., 2021).

7.3 Developing personalized approaches to behavior management

The integration of genetic information with behavioral assessments can lead to personalized approaches to

behavior management in companion animals. By understanding the genetic predispositions of individual animals, tailored interventions can be developed to address specific behavioral issues, enhancing animal welfare and owner satisfaction. This approach can be particularly beneficial in managing behavioral disorders, where genetic insights can inform the selection of appropriate training methods or therapeutic interventions. Personalized behavior management strategies can also aid in the selection and breeding of animals with desirable traits, promoting better compatibility between pets and their owners (Mazzatenta et al., 2017).

8 Conclusion

Behavioral genetics research in companion animals, particularly dogs, has revealed significant insights into the heritability and genetic basis of behavioral traits. Studies have shown that while many behavioral traits are heritable, breed alone explains only a small portion of behavioral variation, indicating a complex interplay between genetics and environment. The genetic architecture of these traits is often polygenic, with individual genomic regions having small effects. Research has also highlighted the importance of considering a wide range of breeds and mixed-breed dogs to fully understand the genetic influences on behavior.

Future research should aim to expand the diversity of dog populations studied, including mixed-breed and non-traditional breeds, to gain a more comprehensive understanding of genetic influences on behavior. There is also a need for larger datasets and longitudinal studies to better quantify genetic variance and identify specific genes involved in behavioral traits. Practical applications of this research include improving breeding programs by selecting for desirable behavioral traits and enhancing animal welfare through better understanding of genetic predispositions to certain behaviors.

The study of behavioral genetics in companion animals holds significant potential for improving animal welfare. By understanding the genetic underpinnings of behavior, we can make informed decisions about breeding and management practices that promote positive behavioral outcomes. This knowledge can also aid in the development of targeted interventions for behavioral disorders, ultimately enhancing the quality of life for companion animals and their human companions.

Acknowledgments

We extend our heartfelt appreciation to Dr. Meng for her invaluable guidance, insightful suggestions, and dedicated contributions during the study's finalisation.

Conflict of Interest Disclosure

Author affirms that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

References

- Alvarenga A.B, Oliveira H., Chen S., Miller S., Marchant-Forde J., Grigoletto L., and Brito L., 2021, A Systematic review of genomic regions and candidate genes underlying behavioral traits in farmed mammals and their link with human disorders, *Animals*, 11(3): 715.
<https://doi.org/10.3390/ani11030715>
- Bengston S.E., Dahan R., Donaldson Z., Phelps S., Van Oers K., Sih A., and Bell A., 2018, Genomic tools for behavioural ecologists to understand repeatable individual differences in behaviour, *Nature Ecology and Evolution*, 2(6): 944-955.
<https://doi.org/10.1038/s41559-017-0411-4>
- Broom D., 2015, New research relevant to companion animal welfare, *Companion Animal*, 20: 548-551.
<https://doi.org/10.12968/COAN.2015.20.10.548>
- Bubac C., Miller J., and Coltman D., 2020, The genetic basis of animal behavioural diversity in natural populations, *Molecular Ecology*, 29: 1957-1971.
<https://doi.org/10.1111/mec.15461>
- Fallahi M., Masoudi A., and Torshizi R., 2024, Genetic variants in the TAC1 transcriptional regulatory region affect on trainability and excitability levels in Belgian Malinois dogs, *Veterinary Medicine and Science*, 10(1): e1346.
<https://doi.org/10.1002/vms3.1346>
PMID: 38227710 PMCID: PMC10790320
- Grandin T., eds, 2013, *Genetics and the behavior of domestic animals*, Academic Press, Fort Collins, Colorado, USA, pp.23-31.
<https://doi.org/10.1016/c2011-0-07148-x>
- Grandin T., and Deesing M., 2014, *Genetics and animal welfare*, Academic Press, Fort Collins, Colorado, USA, pp.435-472.
<https://doi.org/10.1016/B978-0-12-394586-0.00012-3>

- Hecht E., Zapata I., Alvarez C., Gutman D., Preuss T., Kent M., and Serpell J., 2021, Neurodevelopmental scaling is a major driver of brain–behavior differences in temperament across dog breeds, *Brain Structure and Function*, 226: 2725-2739.
<https://doi.org/10.1007/s00429-021-02368-8>
- Ilska J., Haskell M., Blott S., Sánchez-Molano E., Polgár Z., Lofgren S., Clements D., and Wiener P., 2017, Genetic characterization of dog personality traits, *Genetics*, 206: 1101-1111.
<https://doi.org/10.1534/genetics.116.192674>
- Inoue-Murayama M., 2012, Genetic polymorphism as a background of dog behavior, *Japanese Journal of Animal Psychology*, 62: 91-99.
<https://doi.org/10.2502/JANIP.62.1.2>
- Jensen P., 2018, Genetics and genomics of animal welfare, 25-48.
<https://doi.org/10.1016/B978-0-08-101215-4.00002-X>
- Kent C., Tiwari T., Rose S., Patel H., Conflitti I., and Zayed A., 2019, Studying the genetics of behavior in the genomics era, *Encyclopedia of Animal Behavior*, 2019: 223.
<https://doi.org/10.1016/B978-0-12-809633-8.90054-2>
- Krüger O., Korsten P., and Hoffman J., 2017, The rise of behavioral genetics and the transition to behavioral genomics and beyond, *American Psychological Association*, pp.365-379.
<https://doi.org/10.1037/0000011-018>
- Lin X.F., 2024, Adaptive strategies of mammals to changing environments: insights from behavioral and physiological studies, *International Journal of Molecular Zoology*, 14(3): 182-196.
<https://doi.org/10.5376/ijmz.2024.14.0017>
- Lord K., Chen F., and Karlsson E., 2024, An evolutionary perspective on dog behavioral genetics, *Annual Review of Animal Biosciences*, 2024: 13.
<https://doi.org/10.1146/annurev-animal-111523-101954>
- Mazzatenta A., Carluccio A., Robbe D., Giulio C., and Cellerino A., 2017, The companion dog as a unique translational model for aging, *Seminars in Cell and Developmental Biology*, 70: 141-153.
<https://doi.org/10.1016/j.semedb.2017.08.024>
- Morrill K., Hekman J., Li X., McClure J., Logan B., Goodman L., Gao M., Dong Y., Alonso M., Carmichael E., Snyder-Mackler N., Alonso J., Noh H., Johnson J., Koltoukian M., Lieu C., Megquier K., Swofford R., Turner-Maier J., White M., Weng Z., Colubri A., Genereux D., Lord K., and Karlsson E., 2022, Ancestry-inclusive dog genomics challenges popular breed stereotypes, *Science*, 376(6592): eabk0639.
<https://doi.org/10.1126/science.abk0639>
- Per J., and Dominic W., 2013, *Behavioral Genetics and Animal Science*, Academic Press, Fort Collins, Colorado, USA, pp.41-80.
- Petková B., Skurková L., Florián M., Slivková M., Kasičová Z., and Kottferová J., 2024, Variations in canine behavioural characteristics across conventional breed clusters and most common breed-based public stereotypes, *Animals*, 14(18): 2695.
<https://doi.org/10.3390/ani14182695>
PMID: 39335284 PMCID: PMC11429495
- Plassais J., Kim J., Davis B., Karyadi D., Hogan A., Harris A., Decker B., Parker H., and Ostrander E., 2019, Whole genome sequencing of canids reveals genomic regions under selection and variants influencing morphology, *Nature Communications*, 10(1): 1489.
<https://doi.org/10.1038/s41467-019-09373-w>
PMID: 30940804 PMCID: PMC6445083
- Riser M., Leighton E., Russenberger J., Fragomeni B., and Moser C., 2023, 189 Single-step gblup evaluation for behavioral traits in labrador retrievers used as guide dogs, *Journal of Animal Science*, 101(Supplement_3): 96-97.
<https://doi.org/10.1093/jas/skad281.118>
- Rydhmer L., and Canario L., 2014, *Behavioral genetics in pigs and relations to welfare*, Academic Press, Fort Collins, Colorado, USA, pp.397-434.
<https://doi.org/10.1016/B978-0-12-394586-0.00011-1>
- Sanders A.R., Bhongir N., Vonholdt B., and Pellegrini M., 2022, Association of DNA methylation with energy and fear-related behaviors in canines, *Frontiers in Psychology*, 13: 1025494.
<https://doi.org/10.3389/fpsyg.2022.1025494>
PMID: 36591016 PMCID: PMC9794564
- Shan S., Xu F., and Brenig B., 2021, Genome-wide association studies reveal neurological genes for dog herding, predation, temperament, and trainability traits, *Frontiers in Veterinary Science*, 8.
<https://doi.org/10.3389/fvets.2021.693290>
- Sonntag Q., and Overall K.L., 2014, Key determinants of dog and cat welfare: behaviour, breeding and household lifestyle, *Rev. Sci. Tech.*, 33(1): 213-220.
<https://doi.org/10.20506/RST.33.1.2270>
- Toth A., and Rehan S., 2019, Evolutionary behavioral genetics, *Encyclopedia of Animal Behavior*, 2: 73-80.
<https://doi.org/10.1016/b978-0-12-809633-8.90060-8>
- Turcsán B., Kubinyi E., and Miklósi Á., 2011, Trainability and boldness traits differ between dog breed clusters based on conventional breed categories and genetic relatedness, *Applied Animal Behaviour Science*, 132: 61-70.
<https://doi.org/10.1016/J.APPLANIM.2011.03.006>

- Walton A., Sheehan M.J., and Toth A., 2020, Going wild for functional genomics: RNA interference as a tool to study gene-behavior associations in diverse species and ecological contexts, *Hormones and Behavior*, 124: 104774.
<https://doi.org/10.1016/j.yhbeh.2020.104774>
PMID: 32422196
- York R., 2018, Assessing the genetic landscape of animal behavior, *Genetics*, 209: 223-232.
<https://doi.org/10.1534/genetics.118.300712>
- Zapata I., Lilly M., Herron M., Serpell J.A., and Alvarez C., 2020, Genetic testing of dogs predicts problem behaviors in clinical and nonclinical samples, *BMC Genomics*, 23(1): 102.
<https://doi.org/10.1186/s12864-022-08351-9>
PMID: 35130840 PMCID: PMC8819838
- Zapata I., Serpell J., and Alvarez C., 2016, Genetic mapping of canine fear and aggression, *BMC Genomics*, 17: 572.
<https://doi.org/10.1186/s12864-016-2936-3>
PMID: 27503363 PMCID: PMC4977763
- Zhang A.T., 2024, Research on the role of DNA methylation in the epigenetic regulation mechanism of Pomeranian dogs, *Animal Molecular Breeding*, 14(1): 72-81.
<https://doi.org/10.5376/amb.2024.14.0009>
- Zhang Z., Khederzadeh S., and Li Y., 2020, Deciphering the puzzles of dog domestication, *Zoological Research*, 41: 97-104.
<https://doi.org/10.24272/j.issn.2095-8137.2020.002>

Disclaimer/Publisher's Note



The statements, opinions, and data contained in all publications are solely those of the individual authors and contributors and do not represent the views of the publishing house and/or its editors. The publisher and/or its editors disclaim all responsibility for any harm or damage to persons or property that may result from the application of ideas, methods, instructions, or products discussed in the content. Publisher remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.