The Pennsylvania State University

The J. Jeffrey and Ann Marie Fox Graduate School

THE COGNITIVE AND STRESS-RELATED ROOTS OF DOG DOMESTICATION: A BEHAVIORAL, PHYSIOLOGICAL, AND MICROBIAL FRAMEWORK

A Dissertation in

Anthropology

by

Kyle Cristofer Marcusson Smith

Submitted in Partial Fulfillment
of the Requirements
for the Degree of

Doctor of Philosophy

August 2025

The dissertation of Kyle Cristofer Marcusson Smith was reviewed and approved by the following:

George H. Perry
Professor of Anthropology and Biology
Dissertation Advisor
Chair of Committee

Laura S. Weyrich
Associate Professor of Anthropology and Bioethics

Mary K. Shenk
Associate Professor of Anthropology, Demography, and Asian Studies

Nancy A. Dreschel
Associate Teaching Professor of Small Animal Science

Brian A. Hare
Professor of Evolutionary Anthropology
Duke University
Special Member

Timothy Ryan
Professor of Anthropology
Head of the Department of Anthropology

ABSTRACT

Domestic dogs have lived among humans for tens of thousands of years. They successfully spread to human societies globally and have been humans' hunting aids, livestock guardians, and companions. How did dogs become so well-adapted to living among and cooperating with humans? The major differences dogs show from wolves involve advanced social cognition, reduced stress responses, and dietary shifts towards human-like diets. Within dogs, humans, and other animals, social relationships, chronic stress, and diet are all important determinants of fitness. This dissertation investigates the relationships among dogs' cognition, physiological markers of stress, behavior, and microbiomes as potential selective pathways shaped during domestication, with a major goal of validating the measures used to assess these traits. To validate whether cognitive tasks capture meaningful variation in real-world behavior, I first compare dogs' cognition, measured at home by their owners as part of a large-scale citizen science project, to owner-reported surveys of everyday behavior. The results show that performance on cognitive tasks corresponds to important behavioral traits, such as a gesture comprehension task correlating with dogs' communication skills and a memory task correlating with their ability to recall information in daily life. I then extend this analysis by comparing additional cognitive tasks to owner surveys and direct observations of behavior in an off-leash dog park. Interestingly, a task traditionally interpreted as measuring inhibitory control was inversely associated with ratings of dogs' training focus, suggesting it may instead capture aspects of motivation. I next evaluate the relationship between dogs' salivary and hair cortisol levels and measures of acute and chronic stress in order to assess the validity of cortisol as a physiological marker. The results suggest that cortisol may be over-relied upon as an indicator of stress and is likely more appropriate for measuring acute rather than chronic stress. Finally, I explore factors associated with variation in dogs' oral and gut microbiomes. There are weak associations of microbiome composition with social and stress-related factors, as well as a clear association with age. Overall, through the validation of cognitive, behavioral, and stress-related measures used to study dogs, this dissertation contributes to the interpretation of research on dog domestication and intraspecies variation. It also offers methodological recommendations for future studies and lays the foundation for exploring dogs as a model for how social relationships and stress influence both canine and human health.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ACKNOWLEDGEMENTS

At first glance, this is a dissertation about dogs. However, taking a step back, I view it as really being a dissertation about our social relationships with others. The path that led to me studying dogs started with an interest in what makes us human. I think the most fundamental piece of that has to do with our social ties to others. A single human growing up alone in social isolation would not be capable of accomplishing anything noteworthy. What makes humans so fascinating is our propensity for learning culturally from others and our ability for complex communication and cooperation. A desire to understand these abilities better is what drew me to anthropology from a very young age. It is also what made me decide to study dogs even though, at that point in time, I had never had my own dog. Dogs form close social bonds with people around the world, despite not having the close genetic relationship with humans that could cause kin selection to be involved. Through domestication, the social relationships between dogs and humans have exerted selective pressures that shaped the course of dogs' evolution and endowed them with heightened abilities for communicating with another species. We can surely glean some fascinating insights into what it means to be human and the power of social relationships by studying a species that has evolved to form social relationships with humans.

With that in mind, it is only fitting to begin this dissertation with a reflection on a few of the many social relationships that were vital to helping me complete the research described herein.

The most fitting place to start is to express my deep appreciation for my dog Gali and my cat Tuli. They taught me so much about the deep love and affection that can transcend even the bounds of species. Tuli encouraged me to get to work by waiting near my office each morning, meowing, and excitedly following me to my computer, while also reminding me to take a break now and then to dangle string for her. Gali was the first dog I ever had, turning me from a dogless dog researcher to an anthropological participant-observer at the dog park, able to relate to people's stories about their dogs by sharing a few of my own. She was the perfect demo-dog for my outreach events at AnthroFest, the Grange Fair, and several local schools, helping me demonstrate how we study dog cognition and educating the public. Tuli's and Gali's unwavering love and affection helped me get through the stressful moments of my Ph.D. and served as a reminder of how fascinating and exciting it is to explore humans' relationships with domesticated animals.

I would like to thank my parents, Lisa Marcusson and Bryant Smith, for their love and support for my entire life. They always encouraged my interest in animals and anthropology, which led me to where I am today. Their hard work and sacrifices enabled me to follow my dreams and become a scientist.

I am extremely grateful to Dr. George "PJ" Perry for taking me in as a member of his lab despite barely knowing me, already having quite a few students, and having little methodological overlap with my project. Nevertheless, he has been a very supportive advisor in helping me push this dissertation to the finish line. His methodologically rigorous mindset has given helpful insights that strengthened my research. Through a system of weekly updates at lab meetings and in documents, PJ cultivates a lab environment where everyone cares about one another, knows what other lab members are working on and how they are doing personally, and where everyone is held accountable to a high standard for making research progress on a regular basis. This was exactly the kind of environment I needed for the conclusion of my Ph.D. Every interaction I have had with PJ makes it clear he cares about his graduate students as people and cares about ensuring that they conduct high-quality research. I am lucky to have him as my dissertation advisor.

Dr. Brian Hare has had a profound impact on my trajectory as a scientist and a person. Attending his class and lab meetings as an undergrad taught me a lot about the evolution of cognition and how to study it. Due to a fortuitously timed email, I wound up working as his lab manager for two years, over which time he was a key mentor to me. My time in the Duke Canine Cognition Center working with dogs and wolves is the reason I study dogs today. Both during my time as his lab manager and during graduate school, I could always count on Brian for scientific, career, and life advice. His insights into my dissertation research as a committee member were vital for shaping this dissertation. Brian's work developing Dognition and his generosity in allowing me to analyze this dataset were particularly important for the third chapter.

The research in this dissertation would have been impossible without the support of Dr. Nancy Dreschel. When I joined the Penn State Anthropology Department, I had not realized that there were a variety of difficulties and hurdles involved in being the only person in my department who studies dogs. By asking around about any other dog researchers at Penn State, I discovered Nancy and her research on dog salivary cortisol, and I quickly realized she would be the ideal outside-unit committee member for me. Nancy went well above and beyond what would be expected of a committee member and provided crucial support that enabled me to carry out my research. She served as the Principal Investigator for my IACUC and IRB protocols. She even secured a dedicated lab space for me in the Almquist Research Center, where I could bring in dogs for cognitive testing. Nancy was my go-to expert on both the theoretical and practical aspects of salivary cortisol, teaching me how to swab the dogs, how to design my study to reduce confounds, and how to make sense of my results.

Dr. Laura Weyrich was extremely generous with her time and resources to enable me to study the canine microbiome. She took the time to meet with me to go over the project, train me in lab methods, review my analysis code, and more. Laura also generously covered most of the costs associated with extracting, amplifying, and sequencing the DNA from my dog oral microbiome samples. She helpfully provided access to her lab resources, including freezer space, computing cluster resources, and extraction kits. My conversations with Laura helped teach me the kinds of questions I should be asking about the dog microbiome and what the possibilities were for analyzing it.

From the beginning of my interview at Penn State when I had breakfast with Dr. Mary Shenk, it was clear that she is a very warm and talented person. In the Practicum and especially Proposal Writing courses, she provided detailed and insightful feedback that strengthened my research design as well as those of the rest of my cohort. I learned a lot from her about study design and about applying for research funding. After joining my committee, she continued to provide advice about survey design that improved my research.

In addition to my committee, many other individuals provided me with the scientific and logistical support needed to do this research. Dr. Aashish Jha's excited offer to collaborate with me held up even after it became clear I would not be studying free-ranging Australian dogs. He provided guidance to help me sample dog feces, and his lab paid for and performed the DNA extraction, amplification, and sequencing of the gut microbiome samples. Arya Gautam was a critical collaborator from this lab, spearheading a comparison of dog gut microbiomes from around the world, which my samples are but a single part of. On the oral microbiome side, Nicole Moore took the time to train and oversee me in the laboratory techniques for extracting DNA, and she handled the sequencing of these samples. Dr. Doug Bird and Dr. Rebecca Bliege Bird admitted me to the department and helped get me started on my research. Dr. Mark Shriver was generous in letting me borrow various supplies from his lab, such as an iPad for conducting my surveys and a tripod for holding a sign to recruit participants. My request for permission to run around the dog park filming dogs and collecting their feces and saliva was certainly an unusual one, so I am grateful to the various individuals who heard me out and worked with me to allow this project to proceed. I would like to thank the government of Ferguson Township and the Centre Region Parks & Recreation (in particular, Director of Parks & Recreation Pam Salokangas) for permission to conduct research at Tudek Dog Park. I would also like to thank the members of Penn State's IACUC and IRB, especially Melanie Lucas and Jake Werner, for helping me navigate the process of getting an atypical research project approved.

The third chapter of my dissertation uses data from Dognition. Dognition was co-founded by Dr. Brian Hare and Vanessa Woods. The scientific advisory board also includes Dr. Juliane Kaminski, Dr. Ádám Miklósi, Dr. Laurie Santos, Dr. Josep Call, and Dr. Richard Wrangham. The dataset is the fruit of their hard work as well as the contributions of thousands of citizen scientists and their dogs. I am grateful to everyone who contributed to this project and for the chance to analyze this dataset.

This research was funded by several sources at the Pennsylvania State University. The Center for Human Evolution and Diversity funded two seed grants that were invaluable in completing this work. Two Hill Fellowship grants and one Research and Graduate Studies Office Dissertation Support grant also funded this research. The findings and conclusions in this dissertation do not necessarily reflect the views of the funding agencies.

I am indebted to the many humans and dogs who participated in this research. I enjoyed becoming part of the community at Tudek Dog Park and getting to know the other attendees. Many people volunteered their time to allow their dogs to participate. It was great to continue to see many of them over time as I returned to Tudek. I am especially grateful to my various anthropology colleagues and their dogs for being pilot subjects to help me get my data collection system working smoothly: Dr. Rebecca Bliege Bird, Dr. Doug Bird, Tali, and Nala; Grace Bowland and Margo; Chloe McGuire and Popcorn; Brock James, Kaley Tucker, Belle, and Gus; and Rachel Palkovitz and Fern.

The other students of the Perry Lab and Hare Lab provided helpful feedback and encouragement at lab meetings. Maggie Hernandez, Rachel Palkovitz, Ebony Creswell, Laurel Moyse, Natalia Grube, and Sara Gutierrez provided comments on my written lab updates and on my presentations in lab meetings, and they made me feel welcome when switching into the Perry

Lab. Vanessa Woods, Aleah Bowie, Wen Zhou, Hannah Salomons, Morgan Ferrans, Gabi Venable, and of course Congo made the Hare Lab a great environment to be a part of both before graduate school as well as during it, on my attendance of Zoom lab meetings, occasional visits, and eventual move to North Carolina. In addition to the Perry and Hare Labs, I had weekly dog lab meetings with Mia Konzelmann, Emely Carvajal, Paige Murgas, and Sydney Ortega. They helped explore the data with me, discussed papers, and joined me in science outreach.

The administrative staff at the Penn State Department of Anthropology are key to keeping the department running. In particular, Audrey Chambers has been a constant pillar of the department from my initial interview to the present. She was always someone I could go to with any question, knowing that she would either know the answer or be able to find out. Tess Wilson was a tremendous help with figuring out how to use my CHED funds and make the required purchases. Devin Sherman, Morgan Wellman, Kate Nelson, Robin Kephart, and Betty Blair have all helped me overcome various administrative hurdles over the years.

I cherish the friends I have made during graduate school, who greatly improved the experience for me and provided companionship and advice. Kayley Tucker and Brock James were amazing trivia teammates, giving me something to look forward to every week. Makenna Lenover, Kara Peters, Joon Hwang, and Sterling Wright were great cohort members, and I enjoyed spending time with them in and out of class and watching their projects develop over time. Sara Gutierrez never tired of seeing photos of Gali and Tuli and helped us out by watching them when needed. Laura Perez and Melina Porro were always a joy to talk to and even helped run the Stories Under the Sky program. Christine Ta, Rachel Palkovitz, and Maggie Hernandez were great to hang out with inside and outside of work. Outside of Penn State, my friends Abdul Rahman Latif and Rifat Rahman were always a phone call away when I needed them, and they even made the trek out to the middle of Pennsylvania to spend time with me.

Last but not least, I am deeply grateful to my wonderful and loving partner, Abby Gancz. My dog park project had its genesis when we visited Tudek Dog Park together to pet some dogs. By that point, it was becoming clear that my original plans to study free-ranging dogs in Australia, delayed by the pandemic and other logistical hurdles, were never going to come to fruition. Watching all the dogs run around the park interacting with each other and the humans present, I mused to Abby that a dog park would also be an interesting naturalistic setting in which to study dog behavior. On my own, I probably would have done nothing with this idea, but Abby enthusiastically encouraged me to pursue it, resulting in this dissertation. Throughout graduate school, Abby has been my biggest supporter, giving me feedback as I mull over ideas, helping me troubleshoot my microbiome code, commenting on all my drafts, helping me relax with board games and fossil hunting, and believing in me more than I believed in myself. This dissertation would not be what it is without Abby. I have loved building a life together with her and adopting Tuli and Gali, and I am looking forward to our next step of working at NC State together.

Chapter 1

Introduction

Dogs have been living alongside humans for tens of thousands of years (Freedman & Wayne, 2017; Janssens et al., 2018) and have lived on every inhabited continent for thousands of years (Balme et al., 2018; Bergström et al., 2020; Perri et al., 2021). Over this vast period, dogs have taken on a variety of roles, including hunting aids, guard dogs, herders, sled-haulers, and social companions (Chambers et al., 2020; Coppinger & Coppinger, 2000; Lupo, 2019; Perri, 2020; Pitulko & Kasparov, 2017). No other domesticated animal has been so intimately intertwined with humans for as long (MacHugh et al., 2017) nor lived in as many different societies or served such diverse purposes. This raises important questions: How did domestication transform dogs from their ancestral state? What factors enabled them to become so successful at spreading around the world?

Dogs were domesticated from gray wolves approximately 35,000 to 14,000 years ago at one or several locations in Eurasia (Freedman & Wayne, 2017; Shannon et al., 2015; Thalmann et al., 2013; Wang et al., 2016). They subsequently spread throughout Eurasia and into Africa and Australia (Balme et al., 2018; Bergström et al., 2020; Fillios & Taçon, 2016) and accompanied human dispersals into the Americas and Polynesia (Greig et al., 2018; Perri et al., 2021) (Figure 1-1). Evidence dating back thousands of years indicates that dogs were hunting alongside humans (Guagnin et al., 2018), guarding and herding livestock (Coppinger & Coppinger, 2000), and pulling sleds through the snow (Pitulko & Kasparov, 2017). In addition to their utilitarian roles, dogs may also have been beloved companions. Archaeological sites show evidence of deliberate, careful burials of dogs dating back as early as 14,000 years ago, suggesting that ancient humans held affectionate bonds with their dogs (Janssens et al., 2018; Morey, 2006).

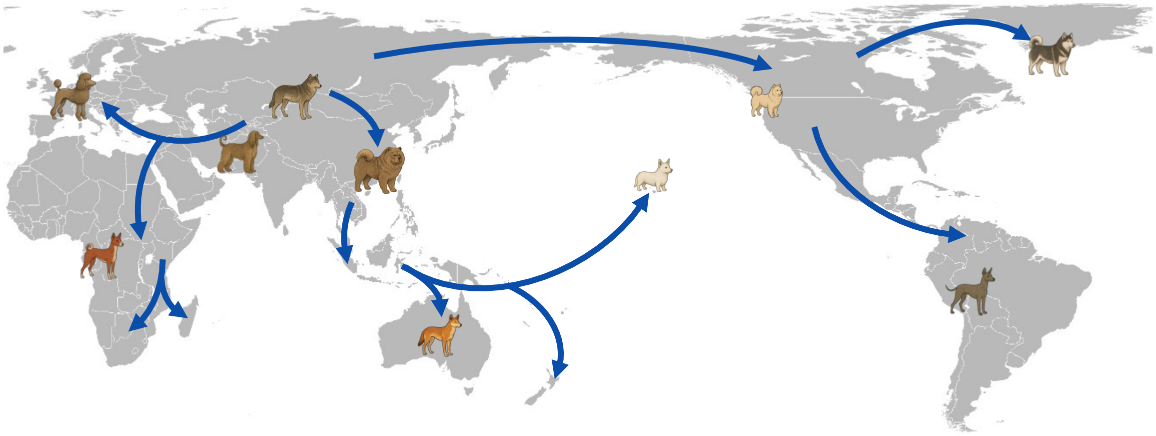

Figure **1-1**: A map of the approximate route of dog dispersal around the world, with distinctive local breeds depicted. Routes depicted are based on information from the published literature (Bergström et al., 2020; Fillios & Taçon, 2016; Freedman & Wayne, 2017; Greig et al., 2018; Perri et al., 2021; Shannon et al., 2015; Thalmann et al., 2013; Wang et al., 2016).

The exact origins of the unique relationship between dogs and humans remains unclear, but there are two main hypotheses for how a subpopulation of wolves evolved into what we now recognize as dogs. The commensal scavenger hypothesis argues that some wolves with little fear of humans were able to exploit a novel niche as scavengers, eating the edible waste of human communities, unlike the more fearful wolves (Serpell, 2021). In contrast, the cross-species adoption hypothesis suggests that humans brought wolf pups into their communities, raising them for a time. Friendlier wolves remained in the community as adults, breeding with others, while more fearful or aggressive wolves either left or were driven out (Serpell, 2021). Although there is insufficient evidence to definitively support one of these hypotheses, both imply similar selective pressures on early dogs: a reduction in fear and reactive aggression was necessary for wolves to live alongside humans without either fleeing or being harmed. Once early dogs evolved calmer temperaments, both natural and artificial selection would have further shaped their adaptations to their new role within human society.

The reduction of fear of humans was likely the critical first step in the domestication of dogs and other mammals. The most universally shared characteristic of domesticated animals is low levels of fear of humans compared to their wild relatives, and this has been argued to be a key factor in the domestication process (Darwin, 1868; Sánchez-Villagra et al., 2016; Zeder, 2012). A prominent difference between dogs and wolves is the generally lower fear of humans exhibited by dogs (Salomons et al., 2021). Genes related to the fight-or-flight response are among the most differentiated between dogs and wolves (Cagan & Blass, 2016). The importance of fearlessness to the domestication of animals is also borne out experimentally. A long-term experiment started in 1950s Siberia involved foxes raised with limited human contact and bred for a lack of fear of humans (Trut et al., 2004, 2009). Within just a few generations, foxes bred for tameness had lost the fear and aggression their ancestors had displayed towards humans (Trut et al., 2009). Eventually, despite only being selected for their behavior, these foxes also began to display phenotypic changes mirroring those seen in domestic dogs relative to wolves (Figure 1-2), such as shorter snouts, smaller teeth, and more frequent occurrence of floppy ears, curled tails, and depigmented patches on their extremities (Trut, 1999; Trut et al., 2004; Wood et al., 2019). While the reasons for these changes are still being explored, one hypothesis suggests that selection for reduced fear and stress response may target the hypothalamic-pituitary-adrenal (HPA) axis, which governs the stress response, via slowed migration of neural crest cells during embryonic development, as these cells give rise to the adrenal glands and other tissues that contribute to the observed phenotypic changes (Wilkins et al., 2014). Thus, the selection for a reduced stress response in early dog domestication may have had pleiotropic effects on other aspects of dogs' phenotypes.

Figure **1-2**: Examples of the traits of the domestication syndrome that often occur in domesticated animals, such as dogs, more frequently than in their wild relatives: floppy ears (left) and a depigmented tail tip (right).

Selection for a modification of dogs' stress response may have been an important selective pressure in dogs' evolution in other ways as well. In addition to making wolves fearless enough to live among humans, a reduced stress response may have imparted health benefits. The stress response activates neuroendocrine pathways that coordinate the body's ability to prioritize a response to the stressor at the expense of less pressing bodily functions (O'Connor et al., 2021). When the stress response is repeatedly activated, the resulting chronic stress can lead to shorter lifespans and worse long-term health outcomes, including persistent inflammation combined with the suppression of other aspects of immune function (Miller et al., 2002; O'Connor et al., 2021). The links between chronic stress and negative health outcomes have been observed in pet dogs, with dogs that are more fearful of strangers having shorter lifespans (Dreschel, 2010). While the significance of a reduced stress response in domesticated animals is well recognized, there has been little discussion on how exactly selection would have acted on this trait. More fearful wolves would likely have avoided human societies, fled after maturing, or acted aggressively and been killed or driven off by humans. However, even after early dogs evolved to be fearless enough to live among humans, there may have been continued selective pressure to reduce the stress response. If living among humans created a state of chronic stress, this could have shortened lifespans and increased illnesses, creating ongoing selective advantages for individuals with less fear and a downregulated stress response.

Besides the reduced fear of humans, several other traits seem to have changed as a result of dog domestication, particularly in the domain of communication with humans. Dogs understand human gestures with remarkable accuracy exceeding that of wolves, even when the wolves have been hand-raised by humans and the dogs have had relatively low levels of human interaction (Hare et al., 2002; Salomons et al., 2021). The same pattern is found in the domesticated foxes relative to a control population of randomly-bred foxes (Hare et al., 2005). Relative to wolves, dogs also make more eye contact with humans when confronted with an unsolvable task, which has been interpreted as a communicative attempt to solicit assistance (Miklósi et al., 2003; Salomons et al., 2021). Furthermore, dogs are capable of learning a wide range of words in human language, with one dog demonstrating the ability to understand over 1,000 words (Pilley & Reid, 2011). Dogs can also distinguish positive and negative emotions in human facial expressions and vocal tones (Albuquerque et al., 2016). Even their facial musculature may have been affected. Dogs have two facial muscles for controlling eyebrow movements that are variable or absent in wolves, which are used in the facial expression often termed “puppy dog eyes”, and it has been argued that these evolved in dogs to facilitate communication with humans (Kaminski et al., 2019; Waller et al., 2013). While it is disputed whether these muscles were selected for in dogs or rather lost in wolves (Cunningham et al., 2024), dogs that frequently use these muscles to make the “puppy dog eyes” facial expression are more quickly adopted in shelters (Waller et al., 2013), so even if these muscles were pre-existing, they may have been evolutionarily co-opted for communicative purposes.

It could be that the communicative abilities of dogs were selected to facilitate cooperation and strengthen social relationships with humans. Dogs' comprehension of human gestures has been linked to the success of military detection dogs at their jobs (MacLean & Hare, 2018). More ancient jobs performed by dogs, such as hunting and hauling, are highly energetically costly (Lupo, 2019). Given that many dogs globally are undernourished and that there are ethnographic records of people provisioning food to successful hunting and hauling dogs (Lupo, 2019), success at these jobs could have exerted a strong selective pressure on dogs over time. If the relationship between dogs' communicative abilities and their success as working dogs extends to jobs like hunting, hauling, and herding, it is plausible that these abilities were selectively honed over thousands of years. Additionally, dogs' communicative abilities could also have been favored if they facilitated the formation of social bonds with humans. Beyond making tangible contributions to subsistence, dogs also serve roles as social companions. Deliberate, careful burials of dogs are seen in various places around the world, and in multiple cultures, dogs are considered kin (Chambers et al., 2020; Morey, 2006). As with chronic stress, the nature of one's social relationships can also affect health and longevity. In a wide range of social mammal species, social connectedness and social status have been found to be some of the biggest predictors of animals' evolutionary fitness (Snyder-Mackler et al., 2020). The experimental manipulation of social status in macaques has been found to alter their gene expression, shifting from antiviral immune functions to antibacterial and pro-inflammatory immune responses (Snyder-Mackler et al., 2016). The hormone oxytocin is often thought of as a social bonding hormone, but it in fact coordinates a whole-body response that is in some ways opposite to the stress response, so it may be functioning to counteract the stress response in the presence of close social relationships (Roney, 2016). If more communicative dogs were more effectively able to form social bonds with humans, perhaps this increased their evolutionary fitness in ways that could select for these abilities. It is noteworthy that oxytocin increases eye contact of dogs with humans (Nagasawa et al., 2009), and measures of social support in dogs are correlated with their health in a cross-sectional sample (McCoy et al., 2023).

The underlying argument of this dissertation is that traits that reduced stress and enhanced social bonding with humans were likely selected during the domestication process due to the impacts of chronic stress and social bonding on health outcomes, and the observed changes in dogs' stress responses and social cognition relative to wolves. One important mechanism by which chronic stress and social bonds could have affected dogs' health is the microbiome. The microbiome is the set of bacteria and other microorganisms that inhabit multicellular organisms' bodies, especially in their guts and mouths (Hou et al., 2022). The microbiome serves various functions for the host, such as facilitating digestion and training the immune system (Valdes et al., 2018). The microbiome has also been linked to systemic health outcomes, both by association and even causally via the translocation of microbes and their metabolites (Gancz & Weyrich, 2023; Hou et al., 2022). There have previously been associations found between the composition of the microbiome and factors like chronic stress or social interactions. Could this be a mechanism by which dogs' chronic stress and social connectedness impacts their fitness? When the gut microbiomes of a whole host of domesticated mammals and their wild relatives are compared, there exists a parallel signature of the composition of the microbiome in domesticates (Reese et al., 2021). The functional significance of this is still being explored, but one area where we have evidence that the microbiome plays a functional role in helping domesticates live with humans is diet. Diet swap experiments in dogs and wolves and in domesticated and wild mice indicate that the gut microbiomes partially converge after time spent consuming the opposite diet (Reese et al., 2021; Xu et al., 2021). The microbiome, especially the gut microbiome, can play a vital role in digestion, as microbes can break down aspects of the diet that the host cannot digest on its own (Valdes et al., 2018). Around the world, dogs often eat similar foods to the human populations they live among (Guiry, 2012, 2013). They have also undergone convergent evolution with humans in terms of their digestion, such as increased copy number of amylase-producing genes in both agriculturalist humans (Perry et al., 2007) and the dogs that live with them (Axelsson et al., 2013), or the evolution of lactase persistence in humans (Ségurel & Bon, 2017) and dogs (Liu et al., 2021) that live in agriculturalist or pastoralist societies that consume dairy. Besides the evolution of the dogs' genetics themselves, changes to dogs' microbiomes may have been a way for them to adapt to novel diets they encountered in the different human societies around the world. For instance, dogs in Bronze Age Italy had not yet evolved increased copy number of amylase genes, but their gut microbiomes were enriched in amylase genes far beyond the level seen in modern dogs (Rampelli et al., 2021).

In sum, major ways domestic dogs differ from wolves include the reduction of their stress response, their increased ability to communicate with humans, and dietary shifts to facilitate the consumption of human food. In various animals, chronic stress is linked to shorter lives and negative health outcomes, and social connectedness is linked to longer lives and better health outcomes. These correlations are likely to be, in part, causal. A reduced stress response in dogs, and any traits such as social cognitive abilities that facilitate the formation of bonds with humans, are likely to have been favored evolutionarily for this reason. The microbiome presents a potential mechanism by which these associations may exist. Additionally, the microbiome offers another way dogs can adapt to the novel diets of human communities, beyond their own genetic evolution.

In this dissertation, I explore the ways in which dogs' social cognition affects their behavior, the relationship of dogs' HPA axis activity to behavioral indicators of stress, and the ways dogs' microbiomes vary between dogs and differ from wolves. In Chapter 2, I begin with a discussion of the ways dog research can contribute to anthropology, arguing that dogs are an understudied topic of variation in humans and their societies and that dogs show great potential as a model for understanding human health and evolution. In Chapter 3, I test whether cognitive tasks designed to measure dogs' social and nonsocial cognitive abilities match their real-world behavior by comparing a large-scale dog cognition citizen science dataset to owner surveys. I expand on this in Chapter 4 by comparing dogs' performance on various cognitive tasks to the real-world behavior I observed in a dog park, as well as to their owners' ratings of their personalities. In Chapter 5, I turn my attention to stress, examining whether cortisol, a widely used proxy for stress, correlates with behavioral measures of stress in either saliva or hair. In Chapter 6, I characterize the gut and oral microbiomes of this sample of dogs, explore whether they have any associations with measures of stress or social interaction, and compare them to published samples from dogs and wolves to see how dog microbiomes differ from those of wolves. Finally, in Chapter 7, I summarize my main findings, discuss their significance and limitations, and offer suggestions for future research.

References

Albuquerque, N., Guo, K., Wilkinson, A., Savalli, C., Otta, E., & Mills, D. (2016). Dogs recognize dog and human emotions. *Biology Letters*, *12*(1), 1–5. https://doi.org/10.1098/rsbl.2015.0883

Axelsson, E., Ratnakumar, A., Arendt, M. L., Maqbool, K., Webster, M. T., Perloski, M., Liberg, O., Arnemo, J. M., Hedhammar, Å., & Lindblad-Toh, K. (2013). The genomic signature of dog domestication reveals adaptation to a starch-rich diet. *Nature*, *495*(7441), 360–364. https://doi.org/10.1038/nature11837

Balme, J., O'Connor, S., & Fallon, S. (2018). New dates on dingo bones from Madura Cave provide oldest firm evidence for arrival of the species in Australia. *Scientific Reports*, *8*(1), 4–9. https://doi.org/10.1038/s41598-018-28324-x

Bergström, A., Frantz, L., Schmidt, R., Ersmark, E., Lebrasseur, O., Girdland-Flink, L., Lin, A. T., Storå, J., Sjögren, K.-G., Anthony, D., Antipina, E., Amiri, S., Bar-Oz, G., Bazaliiskii, V. I., Bulatović, J., Brown, D., Carmagnini, A., Davy, T., Fedorov, S., … Skoglund, P. (2020). Origins and genetic legacy of prehistoric dogs. *Science*, *370*(557–564), 1–7.

Cagan, A., & Blass, T. (2016). Identification of genomic variants putatively targeted by selection during dog domestication. *BMC Evolutionary Biology*, *16*(1), 1–13. https://doi.org/10.1186/s12862-015-0579-7

Chambers, J., Quinlan, M. B., Evans, A., & Quinlan, R. J. (2020). Dog-human coevolution: cross-cultural analysis of multiple hypotheses. *Journal of Ethnobiology*, *40*(4), 414–433. https://doi.org/10.2993/0278-0771-40.4.414

Coppinger, L., & Coppinger, R. (2000). Dogs for herding and guarding livestock. In T. Grandin (Ed.), *Livestock Handling and Transport* (2nd ed., pp. 235–253).

Cunningham, P., Shankar, M., VonHoldt, B., Brzeski, K. E., & Kienle, S. S. (2024). Coyotes can do ‘puppy dog eyes’ too: Comparing interspecific variation in Canis facial expression muscles. *Royal Society Open Science*.

Darwin, C. (1868). *The variation of animals and plants under domestication*.

Dreschel, N. A. (2010). The effects of fear and anxiety on health and lifespan in pet dogs. *Applied Animal Behaviour Science*, *125*(3–4), 157–162. https://doi.org/10.1016/j.applanim.2010.04.003

Fillios, M. A., & Taçon, P. S. C. (2016). Who let the dogs in? A review of the recent genetic evidence for the introduction of the dingo to Australia and implications for the movement of people. *Journal of Archaeological Science: Reports*, *7*, 782–792. https://doi.org/10.1016/j.jasrep.2016.03.001

Freedman, A. H., & Wayne, R. K. (2017). Deciphering the origin of dogs: from fossils to genomes. *Annual Review of Animal Biosciences*, *5*(1), 281–307. https://doi.org/10.1146/annurev-animal-022114-110937

Gancz, A. S., & Weyrich, L. S. (2023). Studying ancient human oral microbiomes could yield insights into the evolutionary history of noncommunicable diseases. *F1000Research*, *12*, 109. https://doi.org/10.12688/f1000research.129036.1

Greig, K., Boocock, J., Allen, M. S., Matisoo-Smith, L., & Walter, R. (2018). Ancient DNA evidence for the introduction and dispersal of dogs (Canis familiaris) in New Zealand. *Journal of Pacific Archaeology*, *9*(1), 1–10.

Guagnin, M., Perri, A. R., & Petraglia, M. D. (2018). Pre-Neolithic evidence for dog-assisted hunting strategies in Arabia. *Journal of Anthropological Archaeology*, *49*(November 2017), 225–236. https://doi.org/10.1016/j.jaa.2017.10.003

Guiry, E. J. (2012). Dogs as analogs in stable isotope-based human paleodietary reconstructions: a review and considerations for future use. *Journal of Archaeological Method and Theory*, *19*(3), 351–376. https://doi.org/10.1007/s10816-011-9118-z

Guiry, E. J. (2013). A canine surrogacy approach to human paleodietary bone chemistry: Past development and future directions. *Archaeological and Anthropological Sciences*, *5*(3), 275–286. https://doi.org/10.1007/s12520-013-0133-8

Hare, B., Brown, M., Williamson, C., & Tomasello, M. (2002). The domestication of social cognition in dogs. *Science*, *298*(5598), 1634–1636. https://doi.org/10.1126/science.1072702

Hare, B., Plyusnina, I., Ignacio, N., Schepina, O., Stepika, A., Wrangham, R., & Trut, L. (2005). Social cognitive evolution in captive foxes is a correlated by-product of experimental domestication. *Current Biology*, *15*, 226–230. https://doi.org/10.1016/j

Hou, K., Wu, Z. X., Chen, X. Y., Wang, J. Q., Zhang, D., Xiao, C., Zhu, D., Koya, J. B., Wei, L., Li, J., & Chen, Z. S. (2022). Microbiota in health and diseases. *Signal Transduction and Targeted Therapy*, *7*(1). https://doi.org/10.1038/s41392-022-00974-4

Janssens, L., Giemsch, L., Schmitz, R., Street, M., Van Dongen, S., & Crombé, P. (2018). A new look at an old dog: Bonn-Oberkassel reconsidered. *Journal of Archaeological Science*, *92*, 126–138. https://doi.org/10.1016/j.jas.2018.01.004

Kaminski, J., Waller, B. M., Diogo, R., Hartstone-Rose, A., & Burrows, A. M. (2019). Evolution of facial muscle anatomy in dogs. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(29), 14677–14681. https://doi.org/10.1073/pnas.1820653116

Liu, Y. H., Wang, L., Zhang, Z., Otecko, N. O., Khederzadeh, S., Dai, Y., Liang, B., Wang, G. D., & Zhang, Y. P. (2021). Whole-genome sequencing reveals lactase persistence adaptation in European dogs. *Molecular Biology and Evolution*, *38*(11), 4884–4890. https://doi.org/10.1093/molbev/msab214

Lupo, K. D. (2019). Hounds follow those who feed them: What can the ethnographic record of hunter-gatherers reveal about early human-canid partnerships? *Journal of Anthropological Archaeology*, *55*(April), 101081. https://doi.org/10.1016/j.jaa.2019.101081

MacHugh, D. E., Larson, G., & Orlando, L. (2017). Taming the past: ancient DNA and the study of animal domestication. *Annual Review of Animal Biosciences*, *5*(1), 329–351. https://doi.org/10.1146/annurev-animal-022516-022747

MacLean, E. L., & Hare, B. (2018). Enhanced selection of assistance and explosive detection dogs using cognitive measures. *Frontiers in Veterinary Science*, *5*(236), 1–14. https://doi.org/10.3389/fvets.2018.00236

McCoy, B. M., Brassington, L., Jin, K., Dolby, G. A., Shrager, S., Collins, D., Dunbar, M., Ruple, A., & Snyder-Mackler, N. (2023). Social determinants of health and disease in companion dogs: a cohort study from the Dog Aging Project. *Evolution, Medicine and Public Health*, *11*(1), 187–201. https://doi.org/10.1093/emph/eoad011

Miklósi, Á., Kubinyi, E., Topál, J., Gácsi, M., Virányi, Z., & Csányi, V. (2003). A simple reason for a big difference: Wolves do not look back at humans, but dogs do. *Current Biology*, *13*(13), 763–766. https://doi.org/10.1016/S

Miller, G. E., Cohen, S., & Ritchey, A. K. (2002). Chronic psychological stress and the regulation of pro-inflammatory cytokines: A glucocorticoid-resistance model. *Health Psychology*, *21*(6), 531–541. https://doi.org/10.1037/0278-6133.21.6.531

Morey, D. F. (2006). Burying key evidence: The social bond between dogs and people. *Journal of Archaeological Science*, *33*(2), 158–175. https://doi.org/10.1016/j.jas.2005.07.009

Nagasawa, M., Kikusui, T., Onaka, T., & Ohta, M. (2009). Dog's gaze at its owner increases owner's urinary oxytocin during social interaction. *Hormones and Behavior*, *55*(3), 434–441. https://doi.org/10.1016/j.yhbeh.2008.12.002

O'Connor, D. B., Thayer, J. F., & Vedhara, K. (2021). Stress and health: a review of psychobiological processes. *Annual Review of Psychology*, *72*, 663–688. https://doi.org/10.1146/annurev-psych-062520-122331

Perri, A. R. (2020). Prehistoric dogs as hunting weapons: the advent of animal biotechnology. In B. Berthke & A. Burtt (Eds.), *Dogs: Archaeology of the Human-Canine Connection Beyond Domestication* (pp. 7–44). University Press of Florida.

Perri, A. R., Feuerborn, T. R., Frantz, L. A. F., Larson, G., & Malhi, R. S. (2021). Dog domestication and the dual dispersal of people and dogs into the Americas. *Proceedings of the National Academy of Sciences*, *118*(6), 1–8. https://doi.org/10.1073/pnas.2010083118

Perry, G. H., Dominy, N. J., Claw, K. G., Lee, A. S., Fiegler, H., Redon, R., Werner, J., Villanea, F. A., Mountain, J. L., Misra, R., Carter, N. P., Lee, C., & Stone, A. C. (2007). Diet and the evolution of human amylase gene copy number variation. *Nature Genetics*, *39*(10), 1256–1260. https://doi.org/10.1038/ng2123

Pilley, J. W., & Reid, A. K. (2011). Border collie comprehends object names as verbal referents. *Behavioural Processes*, *86*(2), 184–195. https://doi.org/10.1016/j.beproc.2010.11.007

Pitulko, V. V., & Kasparov, A. K. (2017). Archaeological dogs from the Early Holocene Zhokhov site in the Eastern Siberian Arctic. *Journal of Archaeological Science: Reports*, *13*(May), 491–515. https://doi.org/10.1016/j.jasrep.2017.04.003

Rampelli, S., Turroni, S., Debandi, F., Alberdi, A., Schnorr, S. L., Hofman, C. A., Taddia, A., Helg, R., Biagi, E., Brigidi, P., D'Amico, F., Cattani, M., & Candela, M. (2021). The gut microbiome buffers dietary adaptation in Bronze Age domesticated dogs. *IScience*, 135907. https://doi.org/10.1016/j.isci.2021.102816

Reese, A. T., Chadaideh, K. S., Diggins, C. E., Schell, L. D., Beckel, M., Callahan, P., Ryan, R., Thompson, M. E., & Carmody, R. N. (2021). Effects of domestication on the gut microbiota parallel those of human industrialization. *ELife*, *10*, 1–27. https://doi.org/10.7554/eLife.60197

Roney, J. R. (2016). Theoretical frameworks for human behavioral endocrinology. *Hormones and Behavior*, *84*, 97–110. https://doi.org/10.1016/j.yhbeh.2016.06.004

Salomons, H., Smith, K. C. M., Callahan-Beckel, M., Callahan, M., Levy, K., Kennedy, B. S., Bray, E. E., Gnanadesikan, G. E., Horschler, D. J., Gruen, M., Tan, J., White, P., VonHoldt, B. M., MacLean, E. L., & Hare, B. (2021). Cooperative communication with humans evolved to emerge early in domestic dogs. *Current Biology*, *31*(July), 1–8. https://doi.org/10.1016/j.cub.2021.06.051

Sánchez-Villagra, M. R., Geiger, M., & Schneider, R. A. (2016). The taming of the neural crest: A developmental perspective on the origins of morphological covariation in domesticated mammals. *Royal Society Open Science*, *3*(6). https://doi.org/10.1098/rsos.160107

Ségurel, L., & Bon, C. (2017). On the evolution of lactase persistence in humans. *Annual Review of Genomics and Human Genetics*, *18*(April), 297–319. https://doi.org/10.1146/annurev-genom-091416-035340

Serpell, J. A. (2021). Commensalism or cross-species adoption? A critical review of theories of wolf domestication. *Frontiers in Veterinary Science*, *8*(April), 1–10. https://doi.org/10.3389/fvets.2021.662370

Shannon, L. M., Boyko, R. H., Castelhano, M., Corey, E., Hayward, J. J., McLean, C., White, M. E., Said, M. A., Anita, B. A., Bondjengo, N. I., Calero, J., Galov, A., Hedimbi, M., Imam, B., Khalap, R., Lally, D., Masta, A., Oliveira, K. C., Pérez, L., … Boyko, A. R. (2015). Genetic structure in village dogs reveals a Central Asian domestication origin. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(44), 13639–13644. https://doi.org/10.1073/pnas.1516215112

Snyder-Mackler, N., Burger, J. R., Gaydosh, L., Belsky, D. W., Noppert, G. A., Campos, F. A., Bartolomucci, A., Yang, Y. C., Aiello, A. E., O'Rand, A., Harris, K. M., Shively, C. A., Alberts, S. C., & Tung, J. (2020). Social determinants of health and survival in humans and other animals. *Science*, *368*(6493), eaax9553. https://doi.org/10.1126/science.aax9553

Snyder-Mackler, N., Sanz, J., Kohn, J. N., Brinkworth, J. F., Morrow, S., Shaver, A. O., Grenier, J. C., Pique-Regi, R., Johnson, Z. P., Wilson, M. E., Barreiro, L. B., & Tung, J. (2016). Social status alters immune regulation and response to infection in macaques. *Science*, *354*(6315), 1041–1045. https://doi.org/10.1126/science.aah3580

Thalmann, O., Shapiro, B., Cui, P., Schuenemann, V. J., Sawyer, S. K., Greenfield, D. L., Germonpré, M. B., Sablin, M. V., López-Giráldez, F., Domingo-Roura, X., Napierala, H., Uerpmann, H.-P., Loponte, D. M., Acosta, A. A., Giemsch, L., Schmitz, R. W., Worthington, B., Buikstra, J. E., Druzhkova, A., … Wayne, R. K. (2013). Complete mitochondrial genomes of ancient canids suggest a European origin of domestic dogs. *Science*, *342*(November), 871–874.

Trut, L. (1999). Early canid domestication: The farm-fox experiment. *American Scientist*, *87*(2), 160. https://doi.org/10.1511/1999.20.813

Trut, L., Oskina, I., & Kharlamova, A. (2009). Animal evolution during domestication: the domesticated fox as a model. *Bioessays*, *31*(3), 349–360. https://doi.org/10.1038/jid.2014.371

Trut, L., Plyusnina, I. Z., & Oskina, I. N. (2004). An experiment on fox domestication and debatable issues of evolution of the dog. *Russian Journal of Genetics*, *40*(6), 644–655.

Valdes, A. M., Walter, J., Segal, E., & Spector, T. D. (2018). Role of the gut microbiota in nutrition and health. *BMJ*, *361*, 36–44. https://doi.org/10.1136/bmj.k2179

Waller, B. M., Peirce, K., Caeiro, C. C., Scheider, L., Burrows, A. M., McCune, S., & Kaminski, J. (2013). Paedomorphic facial expressions give dogs a selective advantage. *PLoS ONE*, *8*(12). https://doi.org/10.1371/journal.pone.0082686

Wang, G. D., Zhai, W., Yang, H. C., Wang, L., Zhong, L., Liu, Y. H., Fan, R. X., Yin, T. T., Zhu, C. L., Poyarkov, A. D., Irwin, D. M., Hytönen, M. K., Lohi, H., Wu, C. I., Savolainen, P., & Zhang, Y. P. (2016). Out of southern East Asia: The natural history of domestic dogs across the world. *Cell Research*, *26*(1), 21–33. https://doi.org/10.1038/cr.2015.147

Wilkins, A. S., Wrangham, R. W., & Tecumseh Fitch, W. (2014). The “domestication syndrome” in mammals: A unified explanation based on neural crest cell behavior and genetics. *Genetics*, *197*(3), 795–808. https://doi.org/10.1534/genetics.114.165423

Wood, E. K., Maddux, S. D., Southard, T. E., Kharlamova, A., Trut, L., & Franciscus, R. G. (2019). The effect of behavioral selection on the dentition of Russian silver foxes and its implications for human dental evolution. *The FASEB Journal*, *33*(1).

Xu, J., Becker, A. A. M. J., Luo, Y., Zhang, W., Ge, B., Leng, C., Wang, G., Ding, L., Wang, J., Fu, X., & Janssens, G. P. J. (2021). The fecal microbiota of dogs switching to a raw diet only partially converges to that of wolves. *Frontiers in Microbiology*, *12*(September). https://doi.org/10.3389/fmicb.2021.701439

Zeder, M. A. (2012). The domestication of animals. *Journal of Anthropological Research*, *68*(2), 161–190.

Chapter 2

Why Anthropologists Should Study Dogs

Introduction

Anthropology is the study of humanity in all its complexity, encompassing cultural diversity (cultural anthropology), human biological evolution (biological anthropology), the lives of past societies (archaeology), and the connections between these fields (Harkin, 2010). While anthropology primarily focuses on humans, research on non-human primates has long played a crucial role in understanding our evolutionary history, as their close genetic relationship to humans makes them valuable models for testing hypotheses about human evolution. Similarly, we argue that greater scientific attention to domestic dogs could offer valuable insights for anthropologists. Dogs have coexisted with humans for thousands of years, adapting to live and work alongside us in ways that reflect deep social and evolutionary ties. Specifically, we identify six areas of anthropological inquiry where the study of dogs holds strong yet underutilized potential to advance the discipline. These are (1) understanding humanity's past, (2) examining humanity's cultural diversity, (3) investigating human impacts on other species, (4) exploring human communication and cooperation, (5) analyzing evolutionary adaptations, and (6) assessing factors that influence human health. We conclude by addressing the limitations, as well as the ethical and practical considerations, that should guide future anthropological research on our canine domesticates.

Understanding humanity's past

Within anthropology, archaeology focuses on reconstructing the lives of past humans. Given their long history alongside humans and their presence in diverse societies, dogs provide a unique opportunity to examine social variation both over time and across cultures. As we will demonstrate, the study of dogs can reveal interactions between societies that might otherwise be difficult to detect. Additionally, in some cases, dogs' remains may serve as a proxy for human remains in destructive analyses, offering an ethical alternative when such studies would otherwise be inappropriate for human samples.

Domestic dogs have been integral to human societies for thousands of years and across much of the world. However, their exact origins remain uncertain, with ongoing debate over when, where, and how many times dog domestication occurred (Larson et al., 2012). Genetic analyses confirm that gray wolves are dogs' closest living relatives, but since the specific ancestral wolf population is unknown, this limits the precision of molecular clock estimates for dating domestication (Larson et al., 2012). Archaeologically, skeletal traits associated with modern dogs and evidence of deliberate burials are key indicators of domestication, though these do not preclude the existence of earlier domesticated dogs (Morey, 2006). One of the earliest unambiguous examples is the Bonn-Oberkassel dog, found in Germany and dated to approximately 14,000 years ago (Janssens et al., 2018). This specimen exhibits both morphological and genetic traits characteristic of dogs rather than wolves. Additionally, it shows evidence of severe pathologies that healed, suggesting human care, and was deliberately buried alongside two humans, further supporting its domesticated status (Janssens et al., 2018). While this specimen confirms the presence of domestic dogs in Europe by 14,000 years ago, dog domestication may have occurred earlier or elsewhere. Proposed origins include Europe, Central Asia, and East Asia, with estimates spanning from 35,000 to 14,000 years ago (Freedman &

Wayne, 2017; Shannon et al., 2015; Thalmann et al., 2013; Wang et al., 2016). Some of this uncertainty arises from the possibility that dog domestication occurred multiple times independently (Larson et al., 2012). Despite these uncertainties, a conservative summary of current evidence suggests that dog domestication took place in Late Pleistocene Eurasia. This would make dogs the first domesticated animal and the only one to predate agriculture (MacHugh et al., 2017).

Once domesticated, dogs quickly spread across human societies worldwide, adapting to diverse climates and subsistence strategies while accompanying humans into new territories. From their initial domestication, dogs soon spread all across Eurasia (Bergström et al., 2020). They were introduced into Egypt from the Middle East and subsequently spread southward through Africa (Bergström et al., 2020). When humans first migrated to the Americas from northeast Asia around 15,000 years ago, dogs are believed to have accompanied them, dispersing alongside human populations throughout North and South America (Perri et al., 2021). Though it took time for dogs to cross the Wallace Line, they eventually reached Australia and New Guinea, likely around 6,000 to 3,000 years ago (Balme et al., 2018; Fillios & Taçon, 2016). The descendants of these early dogs became the New Guinea Singing Dogs and dingoes, which lived in a semi-feral, semi-domestic state—breeding in the wild yet often integrated into human societies for parts of their lives (Meggitt, 1965). Dogs also traveled with people as they expanded across Polynesia (Greig et al., 2018), and their presence may have facilitated the dispersal of the Inuit across the Arctic 1,000 years ago through their roles as sled dogs (Ameen et al., 2019). Even in more modern times, dogs have accompanied humans in exploring extreme frontiers. Early Antarctic expeditions relied on sled dogs for transportation across icy terrain (Murray, 2008). With the dawn of space exploration, dogs were the first mammals sent into space, most famously Laika, as the Soviet space program favored dogs over primates due to their availability and calmer temperaments (Nelson, 2017).

As dogs have spread between societies and accompanied human migrations to new regions, they offer valuable insights for anthropologists studying human movement and trade. One study applied phylogenetic comparative methods to analyze dog-related mythology across cultures, estimating the geographic origin of the ancestral shared narrative. Common themes include dogs as human ancestors, guides to the afterlife, and associations with the star Sirius. The study found that a phylogenetic tree constructed from the similarities between these tales was rooted in Central Asia, aligning with the hypothesized origin of domesticated dogs and suggesting that these stories may trace back to near the origins of dog domestication (D'Huy, 2022). Ancient genomic research on both humans and dogs in the Americas further supports the close relationship between their migrations. The temporal and geographic divergence of human and dog lineages in the Americas is closely correlated, indicating that dogs were already living with the first human settlers in the Americas and spread throughout these continents alongside them (Perri et al., 2021). In Australia and New Guinea, where humans arrived long before dogs, the introduction of the ancestor of dingoes and New Guinea Singing Dogs 6,000 to 3,000 years ago provides evidence of transoceanic contact between the peoples of these regions with Asia, across the Wallace line (Balme & O'Connor, 2016; Fillios & Taçon, 2016). This movement of dogs serves as a key marker of past human interactions and exchanges, reinforcing their value in tracing historical connections between societies.

Archaeologists have employed the Canine Surrogacy Approach to reconstruct past human diets by analyzing the stable isotopes in dog remains as a proxy for human dietary patterns (Guiry, 2012, 2013). Stable isotope analysis of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) can reveal dietary differences between individuals and populations, but because this method involves destructive sampling, there are significant ethical concerns about applying this methodology to human remains, particularly when they are rare or belong to Indigenous or descendant communities opposed to such practices (Guiry, 2012). Since the destructive sampling of dog remains may be less ethically sensitive in these contexts, it can serve as an alternative, provided that dog diets closely reflect those of the humans they lived alongside of (Guiry, 2012, 2013). When the Canine Surrogacy Approach has been applied to compare $\delta^{13}C$ and $\delta^{15}N$ values between human and dog archaeological samples, the results have generally been close, though some exceptions exist (Guiry, 2012). For example, stable isotope analysis of dog remains successfully distinguished Great Lakes communities that consumed maize from those that did not (Edwards et al., 2017). However, there is reason to be cautious with this approach, as several factors could bias results. Misidentification of wild canid remains as dogs, dietary differences between dogs and humans (such as feces consumption), and variations in diets among different distinct dog breeds all pose challenges (Guiry, 2012). A study evaluating this approach among living Nicaraguan horticulturalists found that while dog isotopes were a reasonably accurate proxy for human diets at the site level, they were less reliable at the household level (Perri et al., 2019). Overall, the Canine Surrogacy Approach is a promising tool for dietary reconstruction, but care should be taken to account for potential biases and avoid overinterpretation.

We would like to suggest a few avenues of research that may be particularly fruitful for understanding humans' and dogs' shared past. The field of ancient DNA is currently exploding as more and more genomes of past individuals become available, and this is leading to exciting discoveries about changes experienced by past humans and domesticates (Marciniak & Perry, 2017). As more and more ancient dog genomes become available, this will give researchers new insights into how dogs have changed since they split from wolves and the pathways by which they spread around the world. Comparative mythology is another promising avenue, as myths about dogs are ubiquitous, and new statistical methods applied to comparative mythology databases are enabling us to understand the cultural diffusion of ideas around the world (D'Huy, 2022; D'Huy et al., 2023).

Examining humanity's cultural diversity

The study of human cultural variation and its underlying causes falls within the domain of cultural anthropology. Just as the long-term presence of dogs in human societies makes them valuable subjects for archaeologists, their near-universal presence across cultures allows cultural anthropologists to examine the diverse roles dogs assume in different societies. The ways in which dogs are integrated into human communities offer insights into broader cultural values, belief systems, and economic structures. Additionally, because a few societies were only introduced to dogs in historical times, we have the opportunity to study how the arrival of dogs can influence and reshape societal practices. These cases provide natural experiments in cultural adaptation, allowing researchers to observe how dogs are incorporated into existing worldviews, economies, and social structures over time.

Perhaps no other domesticated animal fulfills as many or as varied a set of functions in human societies as the dog. While most domesticated animals are raised primarily as food, or, occasionally, for specific uses like transportation (Zeder, 2012), dogs have traditionally supported people in a variety of ways across different cultures. They have assisted with hunting, herding, transportation, and alerting people to potential threats, in addition to serving as social companions. Furthermore, dogs continue to fulfill a wide range of specialized roles in modern society, including in therapy, search and rescue, and assistance for people with disabilities (Hall et al., 2021). This versatility underscores the unique and enduring bond between dogs and humans, making them invaluable across both historical and contemporary contexts.

Hunting is one of the oldest and most widespread functions that dogs have served in human societies (Hole & Wyllie, 2007; Perri, 2020). Rock art from as early as 8,000 years ago depicts dogs hunting alongside humans, from the Shuwaymis and Jubbah sites in modern day Saudi Arabia (Guagnin et al., 2018). Additionally, in the early Holocene, dog burials by the

Jōmon culture have been found to spatially and temporally correlate with evidence of the hunting of forest ungulates, which has been interpreted as indicating that dogs played a key role in assisting humans in hunting this prey (Perri, 2016). In anthropology, optimal foraging theory has been effectively used as a framework for modeling humans foraging decisions (Hawkes et al., 2018). The theory predicts that foragers will prioritize targeting food items that maximize energy gained per unit of time spent searching, handling, and processing (Hawkes et al., 2018). This model has been applied to both human hunting both with and without dogs to better understand how dogs impact hunting productivity. Research has shown that dogs can either increase or fail to increase hunting efficiency, depending on factors such as prey type, habitat, and other environmental factors (Koster, 2008; Koungoulos & Fillios, 2020; Lupo, 2017). Dogs improve hunting efficiency by reducing search and handling time through their ability to detect, track, pursue, flush out, trap, capture, and kill prey (Koungoulos & Fillios, 2020; Perri, 2020).

Beyond hunting, dogs have long served in a variety of roles across human societies, including as watchdogs, guardians, herders, and haulers. They can recognize unfamiliar humans or animals and either alert humans or actively defend them from potential threats (Serpell, 2021; Smith & Litchfield, 2009; White, 1972). In societies that rely on livestock, dogs may function as guardians protecting herds from predators or as herders directing livestock (Coppinger & Coppinger, 2000). While modern livestock dogs typically specialize in one of these roles, early artistic depictions of dogs among livestock do not clearly indicate whether they were primarily guarding, herding, or both (Coppinger & Coppinger, 2000). In Arctic regions, the association of dog remains with sled fragments provides evidence that dogs were used for sled-pulling through snow at least 9,000 years ago (Pitulko & Kasparov, 2017). In addition to pulling sleds, dogs have also been used to carry packs and travois, as seen among Indigenous groups in the American Great Plains (Lupo, 2019; Welker & Byers, 2019).

Beyond these common roles, dogs have historically served a diverse array of functions across cultures, both past and present. Dog consumption as food has been traditionally practiced in various societies worldwide, including in North (Durán, 1975) and South America (Cobo, 1893), Europe (Savage, 2012), Africa (Okere, 1980), Asia (Gourou, 1936), and Oceania (Best, 1924). However, strong cultural taboos against eating dogs are also globally widespread (Becher & Schütze, 1960; Ferrars & Ferrars, 1901; Lane, 1952; Pospisil, 1958; Tanaka, 1976). In at least one society, dogs were raised for fabric production. The Coast Salish people of the North American Pacific Northwest traditionally bred a unique woolly dog whose long white hair was woven into blankets and other textiles (Anza-Burgess et al., 2020). These dogs were kept reproductively isolated from hunting dogs, but the breed went extinct after European colonization due to the availability of sheep wool and colonial policies that disrupted Coast Salish communities and targeted traditional practices, including the raising of woolly dogs (Lin et al., 2023). From the 16th to the 19th century in Britain, the turnspit dog was bred to run on a wheel that roasted meat on a spit over the cooking fire, a role that disappeared after technological advances rendered them obsolete (Humphrey, 2024). Charles Darwin even cited the turnspit dog in *On the Origin of Species* as an example of selective breeding producing distinct phenotypic traits (Darwin, 1859). In modern times, the variety of jobs fulfilled by dogs have only expanded. Dogs now work as guide dogs for the blind, hearing dogs for the deaf, service dogs for those with disabilities, and even as contraband detectors (Hall et al., 2021). The sheer diversity of roles that dogs have played across history and cultures underscore their extraordinary adaptability and capacity for cooperation with humans in a wide range of contexts.

In rare cases where cultures acquired dogs in recent historical times, records show that these animals were rapidly integrated into society. In the Andaman Islands, dogs were absent until the 1850s, when pariah dogs from India arrived with the establishment of a penal colony on Great Andaman (Cipriani, 1966). On Little Andaman, dogs were introduced even later, around the start of the 20th century (Cipriani, 1966). In 1928, the Onge people of Little Andaman reportedly had very few dogs, but by the early 1950s, there were reportedly more dogs than humans on the island (Cipriani, 1966). Soon after their introductions, dogs became valuable hunting companions, leading the Andamanese and Onge people to reduce their reliance on shellfish in favor of hunting wild boars which were much easier to hunt with dogs, though this shift coincided with other changes, such as the introduction of guns (Cipriani, 1966). The people of the Andaman Islands reportedly developed a deep fondness for their dogs, pet them, breastfed them, allowed them to sleep in their beds (Cipriani, 1966), gave them individual names (Man, 1932), and even began using the phrase “bibi poiye” (dog not) to refer to the time before colonization (Radcliffe-Brown, 1922).

Similarly, Tasmania had no dogs until European colonists introduced them around the turn of the 19th century (Jones, 1970). Within just a few decades, large packs of dogs became common among Aboriginal Tasmanians, often outnumbering the humans in a band (Jones, 1970). Like the Andamanese and Onge peoples, the Aboriginal Tasmanians were fond of their dogs, named them, and even breastfed puppies. They also relied on dogs for hunting and as sentries, demonstrating the rapid integration of dogs into their society (Jones, 1970).

We suggest that there is great potential for cultural anthropology to look at dogs in both a broad comparative manner and to dive deeply into specific contexts. For instance, Chambers et al. created a database of cross-cultural data on dogs from 144 cultures in the Human Relations Area Files, which is a valuable resource for future studies comparing the role of dogs across societies (Chambers et al., 2020). Intensive studies of dogs in particular societies can allow many different forms of evidence to be drawn together for a more holistic picture. A great example of this is recent work on the Salish woolly dogs that merged ancient DNA, isotopes, interviews of descendant communities, archaeological excavations, and historical records to more completely understand the role of these unique dogs in Coast Salish societies (Anza-Burgess et al., 2020; Lin et al., 2023).

Investigating human impacts on other species

Humans' intensive modification of the environment has been found to exert selective pressure, driving the evolution of a wide range of other species (Perry, 2020; Sullivan et al., 2017). The domestication of animals and plants is, of course, a prime example of how humans have caused other species to evolve, and domestication has been proposed as an important model system for understanding various processes of evolutionary biology (Zeder, 2017). While it remains unclear whether the domestication of dogs originated as a directed process or as a commensal relationship (Serpell, 2021), in either case, it provides an interesting lens through which to examine how humans have exerted selective pressures on other species and how we may continue to do so in the future.

The domestication of dogs marks a pivotal moment in human history as the first instance of domestication. There are two main hypotheses for how this initial domestication event could have occurred: the commensal scavenger hypothesis and the cross-species adoption hypothesis (Serpell, 2021). The commensal scavenger hypothesis proposes that some wolves were attracted to the edible waste left behind by human communities. Over time, the less fearful wolves were able to exploit this new niche, while the more fearful wolves were not. This led to the selection of a new subpopulation of wolves with reduced fear of humans, enabling the eventual formation of close social bonds and practical roles for dogs in human societies (Serpell, 2021). In contrast, the cross-species adoption hypothesis proposes that humans deliberately brought wolf pups into their communities and raised them for a time, with most leaving the human community upon reaching adulthood. However, some of the least fearful and more human-interested wolves remained to live and breed in the human community, leading to the emergence of a new population of dogs (Serpell, 2021). It is still unclear which hypothesis more accurately explains the domestication of dogs. Various modern examples exist of species (including other canids) living near humans that have been argued to have undergone selection on their temperament or dietary tolerance parallel the changes exhibited by dogs (Brooks et al., 2020; Caragiulo et al., 2022; Parsons et al., 2020; Ravinet et al., 2018). Likewise, there are examples of foraging societies raising wild baby animals (Douglass et al., 2021), and the traditional way in which Aboriginal Australians raised dingoes involved dingoes breeding in the bush and humans bringing their pups into human societies (Meggitt, 1965). Regardless of which hypothesis is correct, both note that the initial evolutionary change in wolves that would have been required would be a reduction in their fear of humans followed by the development of an active interest in and attraction to humans.

Central to understanding how humans have exerted selective pressures on domesticates and other animals is the stress response. The main way domesticated animals differ from their wild sister taxa is reduced fear of humans (Sánchez-Villagra et al., 2016; Zeder, 2012). At young ages, even heavily socialized wolf pups are much more wary of humans, especially unfamiliar ones, compared to dog puppies (Salomons et al., 2021). In an experiment in which foxes were artificially selected for their response to humans, foxes lost their fear of humans after just a few generations, and they had longer socialization windows and lower cortisol concentrations (Trut et al., 2009). The genes that distinguish dogs and wolves are particularly concentrated in the adrenaline and noradrenaline biosynthesis pathway, which is part of the stress response (Cagan & Blass, 2016). Stress can be difficult to measure biologically, so it is important to understand the relationship between various biomarkers of stress and their behavioral correlates, as I attempt to do in Chapter 5. With such research in mind, future research should compare pairs of domesticated and non-domesticated animals, such as dogs and wolves, so that we can better understand the evolved differences in their stress response. It is also worth considering that such differences can also be driven partially by selection on wild animals after their divergence from domesticates. The question has been raised of why early humans would tolerate the early ancestors of dogs living among them, given wolves' aggressiveness (Serpell, 2021). However, thousands of years of killing wolves and other wild animals could have exerted a selective pressure to increase their fear of humans. For instance, bolder elk are disproportionately likely to be killed by hunters (Ciuti et al., 2012). Ancient DNA research can compare modern and ancient wolves and dogs, or other animals, and see whether selection on genes related to the stress response has occurred only in domesticated animals or if there has in fact been selection for increased fearfulness in some wild animals due to hunting pressures or other persecution by humans.

Future work on commensal species may generate valuable insights by studying canids that are highly successful in urban environments, such as coyotes and red foxes, and comparing them with dogs. Coyotes in urban environments have been found to have admixture from dogs (Caragiulo et al., 2022), which provides interesting opportunities to see how dog genes affect coyotes phenotypically and whether this helps them thrive as commensal species. Urban red foxes have been found to have more dog-like skull morphology than rural ones (Parsons et al., 2020), so phenotypic convergences may be of interest even without gene flow from dogs. While there has been some work focusing on the behavior of free-ranging dogs (Banerjee & Bhadra, 2021; Paul et al., 2016), such studies are rare, and future studies of free-ranging dogs are likely to give novel insights into the lifestyles of commensal dogs. Anthropological research on wild animals raised by humans should consider how this could exert selective pressures and whether this provides support for a cross-species adoption model of domestication.

Exploring human communication and cooperation

Humans’ advanced social cognition, which allows for complex communication and cooperation, has been proposed as a key defining feature of what makes humans so distinctive (Herrmann et al., 2007). Studying human social cognition and communication can be enriched by comparing it with that of dogs, as dogs exhibit a strong tendency to form close relationships with humans. Their remarkable ability to communicate with humans is believed to have evolved as a result of domestication, making them an intriguing model for understanding the development of social cognition in humans.

In addition to fulfilling concrete functions such as hunting, herding, hauling, and guarding, which directly impact human subsistence, dogs also serve as social companions to humans. Modern polls of people in the United States find that around 85-94% of American dog owners consider their dogs to be a member of the family (Pew Research Center, 2006). However, viewing dogs as social companions and akin to humans is neither idiosyncratic to modern Western societies nor universal across cultures or throughout history. Different cultures categorize the world in diverse ways, and the terms “human” and “person” are not always viewed as synonymous (Chambers et al., 2020; Descola, 2013; Fuentes, 2006; Musharbash, 2017). Some cultures reserve personhood exclusively for humans, while others extend it to a broad range of entities, with some cultures grouping dogs as more similar to humans than to other animals (Chambers et al., 2020; Musharbash, 2017). Across various societies, dogs have been given individual names, considered part of the kin group, provided with burial practices otherwise reserved for humans, and even allowed to sleep alongside humans in their beds (Chambers et al., 2020).

As described above, dogs were the first domesticated animals, spreading through human societies around the world by the mid-Holocene and being rapidly adopted by the few societies that did not have them until recent times. They cooperate with humans to help with subsistence and other tasks, and in many societies, they are regarded as companions and are shown affection. What is it about dogs that makes them so predisposed to spread among human societies and form close relationships with humans?

Various lines of evidence indicate that dogs evolved enhanced abilities to communicate with humans and appear to have evolved to be more similar to humans in several potentially important and informative ways. In particular, dogs outperform their wild relatives, the gray wolves, in understanding human gestures (Hare et al., 2002; Salomons et al., 2021), a difference that is paralleled in experimentally-domesticated foxes compared to a control line of non-domesticated foxes (Hare et al., 2005). Dogs even surpass chimpanzees, our closest evolutionary relatives, in spontaneous gestural comprehension tests (Hare et al., 2002). In addition to understanding human communication, dogs also appear predisposed to generate communication with humans. When presented with a task that they cannot solve without human assistance, dogs make more eye contact with humans than wolves do (Miklósi et al., 2003; Salomons et al., 2021). Compared to wolves, dogs have evolved muscles for raising their eyebrows in a manner that humans respond strongly to, and it has been argued that this has been selected for facilitating communication with humans (Kaminski et al., 2019; Waller et al., 2013), although whether it evolved in dogs or was lost in wolves is disputed (Cunningham et al., 2024). Experimental evidence indicates that dogs can distinguish between positive and negative emotional valences in human facial expressions and vocal tones (Albuquerque et al., 2016). Dogs are also well known for being able to be trained to learn words or commands from humans. Many cultures have been documented to train dogs to respond to specific commands, especially when dogs are performing specific jobs like hunting (Grigson & Elwin, 1949; Raswan, 1947), herding (Vorren et al., 1962), or hauling sleds (Black, 1973; De Coccola et al., 1986). One exceptional dog was even documented to learn and remember the names of over one thousand distinct objects (Pilley & Reid, 2011).

The similarity of dogs' social cognitive abilities to those of humans makes them a particularly attractive model for understanding human social cognition. A comparison of individual differences in the cognition of dogs, chimpanzees, and human infants suggests that the underlying structure of cognitive differences is more similar between human infants and dogs than humans and chimpanzees, with social tasks clustering separately from physical reasoning tasks in humans and dogs but not in chimpanzees (MacLean et al., 2017). Thus, a better understanding of the nature of dogs' cognitive abilities and the correlates of various cognitive tasks may help generate novel insights about the nature of humans' own cognition, especially in the social domain. For that reason, future research should examine the behavioral correlates of dog cognition tasks, as I do in Chapters 3 and 4, which will help clarify what these tasks measure and may therefore contribute to our understanding of human cognition as well.

Understanding the selective pressures operating on dog behavior may help us understand how cognition evolves in dogs and other species. While dog social cognition has been linked to the success of military detection dogs (MacLean & Hare, 2018), future work should look at how the social cognition of dogs affects their performance at more ancient jobs like hunting and herding, as these could have exerted sustained selective pressures on dog cognition over thousands of years. Citizen science projects provide an opportunity to collect cognitive data on more dogs than could possibly be collected by one research team, such as the Dognition project (Stewart et al., 2015). The growing popularity of button-based soundboards among pet dogs is also providing novel opportunities to look at dogs' communicative abilities (Bastos & Rossano, 2023).

Analyzing human evolutionary adaptations

Biological anthropologists are interested in the evolutionary adaptations that humans have, both to specific environments in which some humans live and also the general adaptations shared by all humans that emerged in our species' distant past. As dogs are found across most of the same environmental and lifestyle gradients as humans, they have, in various instances, been found to have evolved similar adaptations. Dogs have also been proposed as a valuable model for understanding the cognitive and behavioral evolution of our species (Hare, 2017; MacLean et al., 2017)

One aspect in which humans and dogs show similarities is in their diet. Humans and dogs have undergone convergent evolution for several digestive adaptations to particular diets. For instance, humans have evolved an increased copy number of the gene for salivary amylase relative to great apes, with agricultural societies exhibiting higher copy numbers on average due to greater starch consumption compared to forager and pastoralist societies (Perry et al., 2007). Similarly, dogs have increased copy number of the gene for amylase in the pancreas compared to wolves (Axelsson et al., 2013). Dog breeds from regions with limited starch in the diet, such as the Arctic, have fewer copies of this gene than those from areas where starch is more commonly consumed (Reiter et al., 2016). Another famous example of recent human dietary evolution is also seen in dogs. In a variety of human societies where people regularly consume dairy products, there has been genetic evolution to produce lactase, the enzyme that breaks down lactose, as an adult (Ségurel & Bon, 2017). Dogs in Europe and the Middle East have also undergone positive selection for an allele of lactase that is believed to increase the expression of this gene, and the timing of the sweep corresponds to the development of dairying in this region (Y. H. Liu et al., 2021). Additionally, dietary adaptations of dogs, mirroring those of humans, can be observed in the gut microbiome. A signature of domestication in the gut microbiome has been identified in various pairs of related domesticated and wild species, including dogs relative to wolves. Dietary swaps and comparisons to human populations indicate that these adaptations may be linked with an industrialized diet (Reese et al., 2021). Like humans, dogs in industrialized societies have less diverse gut microbiomes than those in non-industrialized societies (Yarlagadda et al., 2022). In Chapter 6, I show that the increased abundance of *Lactobacillus* and related taxa in dog guts are some of the most prominent differences from wolf guts. Dogs' gut microbiomes also appear adapt to their diets, as dogs that consume dairy have bacteria with functions for breaking down lactose, a feature not found in other dog populations (Yarlagadda et al., 2022).

These examples of how dogs adapt to new diets through the microbiome as well as through their own genetic adaptations can illustrate potential mechanisms by which new adaptations occur in humans. While humans' evolution of lactase persistence is known to be related to dairy consumption, it is still not fully understood why this has occurred. Some populations (such as central Asians) with high levels of dairy consumption nevertheless have low levels of lactase persistence (Segurel et al., 2020), and dairy consumption existed for thousands of years in Europe before lactase persistence was selected for (Evershed et al., 2022). It has been suggested that particular forms of dairy consumption, such as a reliance on fermentation to partially break down lactose before consumption, could reduce the selective advantage of lactase persistence in certain societies (Segurel et al., 2020), or perhaps that lactase persistence only exerts a strong effect on fitness under conditions of high nutritional or pathogen stress (Evershed et al., 2022). Examining the patterns of when and where dogs evolve lactase persistence could be particularly helpful in disentangling the selective pressures involved (Peng et al., 2023). Evidence from dogs also suggests that the microbiome could play a key role in allowing dietary expansion prior to the initiation of selection on digestion. For instance, ancient DNA from Bronze Age Italian dog coprolites has revealed that these dogs had not yet evolved extra copies of amylase, but their gut microbiomes had microbes that produced alpha-amylase as levels well beyond those seen in modern dogs. This suggests a pathway by which dietary evolution can occur in dogs and other species: changes to the microbiome can allow an animal to digest new foods enough for them to be a component of the diet, and then over time, this opens up the possibility for natural selection to operate on the host animal's own genetic adaptations to the diet. It is possible this pathway could also occur in humans. Individual humans who consume dairy but are not lactase persistent have higher levels of *Bifidobacterium*, which can break down lactose (Goodrich et al., 2017), so perhaps (like dogs' adaptations to starches) humans adapted to consuming lactose initially via the microbiome and then later by their own genetic evolution. Further exploration of this process in dogs may prove illustrative for how such adaptations can occur in humans. Perhaps the *Lactobacillus* in dairy-consuming dog populations contributes to their ability to digest dairy products, especially in individuals without lactase persistence, as discussed in Chapter 6.

Several other genetic variants within dogs have interesting parallels with humans. In high-altitude regions such as Tibet, both dogs and humans have adaptations to chronic hypoxia involving the *EPAS1* gene (Wang et al., 2014). These genes were selected for after introgression from populations that had been present in the region for longer: Denisovans in the case of humans and wolves in the case of dogs (Huerta-Sánchez et al., 2014; Miao et al., 2017). In Nigeria dogs, the *ADGRE1* gene shows evidence of positive selection (Y.-H. Liu et al., 2018). It is believed to protect against a malaria-like disease called canine babesiosis, and *ADGRE1* is also linked to malaria resistance in African human populations (Y.-H. Liu et al., 2018). Additionally, transposon insertions in the *GTF2I* and *GTF2IRD1* genes in dogs have been linked to variation in dogs' friendliness towards strangers, with a strong difference observed between dogs and wolves (VonHoldt et al., 2017). A deletion of this region from humans' genomes cause a condition called Williams-Beuren Syndrome, a condition that results in exceptional outgoing behavior and an indiscriminate attraction to other people (VonHoldt et al., 2017).

Some researchers have hypothesized that both humans and dogs have undergone convergent evolution due to selection against aggression, a concept referred to as the human self-domestication hypothesis (Hare, 2017; Wrangham, 2019). As early as Darwin, it has been noted that particular traits tend to recur in domesticated animals compared to their wild counterparts, such as reduced fear and aggression, smaller teeth, shorter snouts, and increased frequency of floppy ears and tails and of depigmented patches (Darwin, 1868; Trut et al., 2009; Wilkins et al., 2014). This so-called "domestication syndrome" has drawn attention, in part due to a long-running experiment to domesticate foxes. Starting in 1959 in the Soviet Union, initially Dmitry Belyaev and later Lyudmila Trut oversaw a project in which foxes were raised with minimal human contact, tested for their response to humans, and the few that responded most positively towards humans were selected for breeding (another line of foxes was bred randomly as a control group) (Trut, 1999). After four generations, there were foxes that lacked any noticeable fear of or aggression towards humans, and in subsequent generations, they began to show actively positive responses towards humans (Trut et al., 2004). Even though the foxes were only selected on the basis of their behavioral responses towards humans, other changes were observed that paralleled those seen in dogs and other domesticates relative to their wild counterparts, including reduced snouts and teeth and higher incidence of curled tails, floppy ears, and depigmented patches (Trut, 1999; Trut et al., 2004; Wood et al., 2019). While the cause of this domestication syndrome remains unclear, one hypothesis is that domestication selects for a reduction of the stress response and therefore for changes to the HPA axis, and that slowing the migration of neural crest cells during embryonic development may affect both the HPA axis as well as other physical traits implicated in the domestication syndrome (Wilkins et al., 2014). The human self-domestication hypothesis proposes that humans have undergone selection against aggression, which as a result, caused elements of the domestication syndrome, such as reduced prognathism and smaller teeth (Cieri et al., 2014; Hare, 2017; Theofanopoulou et al., 2017; Wrangham, 2019). While the human self-domestication hypothesis has been criticized as lacking sufficient evidence and clarity, it generates testable predictions and can continue to be evaluated (Sánchez-Villagra & van Schaik, 2019). In evaluating the human self-domestication hypothesis, comparisons to dogs and wolves may be particularly informative (Hare, 2017).

Future research can utilize the growing number of publicly available dog genomes to look for evidence of selection in dogs and whether this has parallels with human evolution. The Dog10K consortium has published around 2,000 dog genomes, including over 300 breeds and also village dogs from more than two dozen countries, and they plan to raise that sample size to 10,000 (Meadows et al., 2023). As village dogs in different parts of the world may need to solve similar environmental, dietary, and infectious challenges as the local humans, their genetic variation should particularly be explored in more detail. For instance, besides Tibet, humans are known to have high-altitude adaptations in the Andes (Julian & Moore, 2019) and Ethiopian highlands (Scheinfeldt et al., 2012), so dogs in these areas might be found to have similar adaptations, particularly in Ethiopia, where the local wolves are genetically adapted to high altitudes (Mooney et al., 2023) and are able to hybridize with domestic dogs (Gottelli et al., 1994). The microbiomes of dogs also have great potential for future research to examine whether the factors associated with variation of human microbiomes also show evidence of similar patterns in dogs (Yarlagadda et al., 2022).

Assessing factors that influence human health

Human health is a central focus for anthropologists for several reasons. Health plays a significant role in an individual's ability to survive and reproduce, making it deeply connected to evolutionary fitness (Nunn et al., 2015). On a more applied level, improving global health is a key objective of applied anthropology (Janes & Corbett, 2009). We argue that dogs are an underappreciated model for studying human health, offering unique advantages that other commonly studied species do not. This is largely due to the fact that dogs live alongside humans across a wide variety of shared environmental conditions, making them a valuable species for comparative health studies.

Human health can certainly be studied directly in humans, but no other species will ever be a perfect model for human health. Longitudinal studies of humans, while invaluable, can take decades to reveal chronic health outcomes. Additionally, the complexities of human societies introduce many confounding variables, and some experimental interventions are simply not feasible (Vanhooren & Libert, 2013). As a result, researchers often turn to model organisms from other species to study human health (Vanhooren & Libert, 2013). Mice, for example, are among the most commonly used model organisms due to their short generation times and the possibility of tightly controlling and manipulating variables in laboratory settings (Vanhooren & Libert, 2013). However, while laboratory studies on mice are crucial, there are limitations to how their findings can be applied to real-world environments (Garner, 2014). Nonhuman primates, as our closest relatives, also offer valuable insights, particularly from an evolutionary perspective. Although field observations of wild primates have provided important insights into human health (Nunn et al., 2015; Sapolsky, 2004; Snyder-Mackler et al., 2020), these species do not experience the full spectrum of environments and lifestyles that humans do, and as with humans, their long lifespans mean that measuring chronic health outcomes takes a very long time. For these reasons, many anthropological studies on human health would benefit from studying a species that lives alongside humans in diverse contexts, experiencing many of the same environmental conditions, and that has a relatively shorter life history, such as dogs.

Dogs live in environments that are more similar to humans (and across more similar environmental gradients) than any other species, making them unique and ideal models for studying health. Like humans, dogs experience variations in lifestyle factors that are relevant to health, including diet, exercise, social interactions, chemical exposures, pathogen and microbe exposures, climatic conditions, and access to healthcare. A comparison of causes of death in U.S. humans and the diagnoses at the time of death in U.S. pet dogs found that the pathophysiological processes, organ systems, and cancer types occurred at similar rates in both species (with the notable exception of vascular causes of death, which are common in humans but rare in dogs) (Hoffman et al., 2018). Furthermore, the age trajectories (scaled for lifespan) were similar in both species, and the numbers of comorbidities associated with chronic health conditions were correlated (Hoffman et al., 2018). These parallels suggest that dogs are a promising model for how environmental factors affect health and aging (Hoffman et al., 2018; Ruple et al., 2022).

The social determinants of health framework, which examines how social factors like social status, social connectedness, and early life adversity affect health and longevity, has become an important area of study in anthropology (Snyder-Mackler et al., 2020). This framework has recently been applied to pet dogs, revealing that socioeconomic status was positively correlated with the overall health of pet dogs in the U.S. Additionally, social connectedness, specifically as the presence of other dogs in the household, also appeared to influence dog health (McCoy et al., 2023). While this study was cross-sectional and could not eliminate other possible confounding factors (e.g., a more invested owner providing better care for more dogs), these findings align with the larger body of research that social relationships can affect health. Future research should continue to explore how the social relationships of dogs affect their health. Chronic stress and its effects on health also present a meaningful area of investigation in dogs. In humans, lower socioeconomic status has been linked to higher rates of various health conditions, with stress related to low status being a proposed contributing factor (Chetty et al., 2016; Link & Phelan, 1995; Sapolsky, 2004; Snyder-Mackler et al., 2020). In pet dogs, fear of strangers has been associated with significantly shorter lifespans (Dreschel, 2010), further supporting the importance of stress in health outcomes across species. Research on dogs may be particularly informative in this domain. It has been proposed that chronic stress only evolves under certain conditions when it may be adaptive, and that it is less likely to be adaptive in species with short lifespans (Boonstra, 2013). For that reason, dogs may be a better model for chronic stress than mice due to their relatively longer lifespans. Exploration of the ways in which dogs are similar or different from humans may also be informative. For instance, social isolation or low social status in humans and macaques is associated with changes to gene expression in which antiviral functions are downregulated and antibacterial functions are upregulated (O'Connor et al., 2021; Snyder-Mackler et al., 2016). Determining whether this occurs in dogs, for instance when a dog is adopted from a shelter into a stable home, may help determine why such changes occur, such as whether they are widespread in mammals or whether this is the result of changes to the degree of interactions with conspecifics and therefore the risk of viral infections. The ability to quantify stress in dogs is critical for research on how stress affects dogs' health, as explored in Chapter 5 of this dissertation.

Dogs may also be an important model for the role of the microbiome in health. At least on the skin, dogs and humans from the same household have been found to share microbes (Song et al., 2013). Microbes in the gastrointestinal tract and oral cavity are particularly important given their associations with various health conditions (Gancz & Weyrich, 2023; Hou et al., 2022). These associations are in some cases believed to be causal, as microbes and their metabolites can translocate throughout the body and contribute to disease risk (Martinez et al., 2017; Ross et al., 2024). The microbiome may be particularly important in explaining the links between chronic stress and health. Chronic stress can lead to inflammation, which shifts the composition of the microbiome and increases gut permeability, thereby increasing the risk of microbes and their metabolites escaping into the bloodstream (Marwaha et al., 2025). In Chapter 6, I examine the oral and gut microbiomes of dogs with relation to variables related to stress and social interactions in order to explore the associations that exist in dogs. By using dogs as a model for the relationship between the microbiome and health, we can control for the effects of various confounding factors limited to humans while also having a more naturalistic model than laboratory mice. Clinical trials of probiotics in companion dogs may be a useful way to test chronic health outcomes outside of the laboratory while getting results sooner than in human research.

Future research using dogs as a model for human health will have several large-scale longitudinal databases to draw from. The Golden Retriever Lifetime Study tracked 3,000 Golden Retrievers across their lifespans, collecting a wide variety of detailed data about them (Guy et al., 2015). Inspired by this, the ongoing Dog Aging Project is currently collecting genetic, environmental, and health data from thousands of purebred and mixed-breed dogs (Kaeberlein et al., 2016). Rich sources of data such as this will provide opportunities to test the effects of various environmental factors on long-term health outcomes. The nature of pet dogs allows for the possibility of randomized clinical trials to test the effects of interventions that are difficult to test in humans on a reasonable timescale, and these should be considered to better understand causal relationships. As in some cases it can be hard to understand the role of genetics versus environmental factors when health conditions recur within a family, the presence of non-genetically related dogs in the household provides a potentially illuminating basis of comparison.

Limitations and suggestions for future research

Comparative methods are central to anthropology, as they allow researchers to generate and test hypotheses about why particular traits differ across species or cultures (Nunn, 2011). Typically, anthropologists compare humans with other primates (Rodman, 1999), but there is growing recognition that comparisons with species outside of the primate order can also yield valuable evolutionary insights (Palkovitz & Lawler, 2024). Dogs, in particular, are well-suited for anthropological comparison with humans due to their shared environments, diverse breeds, and evolutionary history. Not only can dogs and humans be directly compared, but comparisons within the broad diversity of dogs and other canid species can also be of help for testing anthropological hypothesis. Since dogs are found in nearly all human societies, they provide a unique opportunity to study how different diets, environments, and lifestyle conditions affect health and behavior in both species (Yarlagadda et al., 2022). The diversification of dog breeds is an example of evolutionary adaptive radiation, and indeed the selective breeding of dogs was influential to Darwin in his development of the theory of evolution by natural selection (Darwin, 1859). While the genetic structure and evolutionary history of dog breeds is very different from that of human populations and is therefore not a good model for it (Norton et al., 2019), certain dog breeds have evolved traits that converge with human adaptations to shared conditions, such as adaptations to hypoxia (Wang et al., 2014) or to a starch-rich diet (Axelsson et al., 2013). In studying domestication, dogs provide valuable insights into human evolution and the domestication process itself. For instance, wild canids, particularly gray wolves, the closest living relatives of domestic dogs (Vilà et al., 1997), are commonly compared to dogs to study the effects of dog domestication (Bentosela et al., 2016; Marshall-Pescini et al., 2017; Miklósi et al., 2003; Salomons et al., 2021). Experimental domestication studies, such as the Siberian fox domestication experiment (Trut et al., 2009), also offer a unique comparison for understanding domestication. Dingoes, which descend from domesticated dogs but now breed in the wild and have been described as “untamed” or “feral” (Ballard & Wilson, 2019; Shipman, 2020; Zhang et al., 2020), have also been compared to dogs to study the effects of domestication (Johnston et al., 2017; Smith & Litchfield, 2013). Additionally, several other canid species, such as coyotes and red foxes, have been increasingly common in urban areas and have been proposed to be undergoing some of the same selective pressures as early dogs (Brooks et al., 2020; Parsons et al., 2020). These diverse comparisons provide valuable data for understanding domestication, evolutionary adaptation, and human-canine relationships across time and environments.

As anthropologists are well aware, most psychological and medical research on humans focuses on individuals in industrial societies, primarily in North America and Europe. However, these societies are not representative of the diversity of human lifestyles, and they differ in several substantial ways from how humans lived for most of our species' existence (Henrich et al., 2010). Likewise, most studies of dogs focus on companion dogs in North America and Europe, but these differ from the majority of dogs in several important ways, as typically they are sterilized, receive veterinary care, are fed food specifically for dogs, undergo obedience training, have a recent history of intensive breeding, and live relatively isolated in the family's house (Koster, 2021). Just as anthropologists study humans from a variety of cultures and settings to better understand the full range of the human experience, we encourage anthropologists to expand their focus to include dogs living in diverse contexts. This should encompass dogs in societies with more traditional lifestyles, free-ranging and feral dogs with limited human interaction, and dogs that assist humans in various roles, such as hunting, herding, or other forms of work. By studying dogs in a broader range of environments, we can gain a more comprehensive understanding of the ways in which dogs interact with humans, adapt to different ecological and social conditions, and contribute to human societies in diverse ways.

Although this is not true in all parts of the world, in the US and Europe, most pet dogs are spayed and neutered (Koster, 2021). For studies on dogs in these regions, this limits the ability to use fertility as a measure of evolutionary fitness, so other proxies such as health and longevity become more applicable. Sterilizing dogs also reduces their utility for research on reproductive health, sex differences, and the influence of sex hormones. However, this limitation can still serve as a useful basis for comparison in some cases, as a sample that includes both intact and sterilized dogs would allow for testing the effects of sex hormones. Another important way that pet dogs in the US and Europe differ from most dogs globally and from humans is that Western companion dogs often die due to euthanasia (Pegram et al., 2021), This can limit the direct comparison of their health conditions and lifespan with humans. However, euthanasia typically occurs due to underlying health conditions, which are comparable to human causes of death, and the lifespan of euthanized dogs may be an appropriate comparison for humans' duration of healthy living (Ruple et al., 2022).

We would like to close with some remarks on ethical considerations surrounding research with dogs. First, our suggestion that dogs may be a good model for understanding human health should not be interpreted as a suggestion that dogs should replace mice as laboratory subjects. The advantages to studying dogs as a model for humans come precisely from the fact that they inhabit the same real-world environments that humans do. Furthermore, while the ethical oversight of animal research is the purview of Institutional Animal Care and Use Committees (IACUC; this is specific to the US, but similar bodies in exist in other countries), dog researchers would do well to draw their ethical considerations from research on human infants. The widely recognized ethical principles of animal research (overseen by IACUC and discussed in the *Guide for the Care and Use of Laboratory Animals*) are to minimize the number and complexity of animal subjects and to minimize pain when possible (the Three Rs: replacement, reduction, refinement) (National Research Council, 2011). These principles were often crafted with invasive laboratory research in mind, and while all required regulations should of course be followed, researchers should acknowledge that pet dogs, in some ways, are more similar to human subjects than traditional laboratory animals. The basic principles of Institutional Review Boards (IRBs, which oversee human subjects research in the US), as laid out in the 1979 *Belmont Report*, are respect for persons (treating individuals as autonomous and protecting those with limited autonomy), beneficence (maximizing benefits and minimizing possible harms), and justice (treating people fairly) (National Commission for the Protection of Human Subjects of

Biomedical and Behavioral Research, 1979). The *Belmont Report* notes that while children and infants have limited autonomy and ability to comprehend research projects, they should nevertheless be given the opportunity to choose whether or not to participate in research, to the extent that their cognitive abilities allow (National Commission for the Protection of Human Subjects of Biomedical and Behavioral Research, 1979). In a similar vein, much non-invasive research involving dogs can be designed so that subjects can opt not to participate. For research involving underage children, the informed consent of a parent or legal guardian is required; similarly, a pet dog's legal owner should provide informed consent for their participation in research. When studying dogs in different cultural contexts, it is vital to be sensitive to the specific role that dogs play within those societies. For studies of free-ranging dogs, the appropriate model is non-invasive animal research, involving obtaining local and national permissions and minimizing any disturbance to the animals.

Conclusions

The study of dogs offers a wealth of applications for a broad range of anthropological questions. Given that dogs have lived alongside humans globally for thousands of years, they are a valuable subject of inquiry for archaeologists and cultural anthropologists seeking to understand their roles in human societies across time and cultures. Dog remains, in particular, serve as useful proxies in analyses where human remains may not be viable or appropriate. Dog domestication itself is a fascinating case study that illuminates broader themes of domestication, commensalism, and the impact of humans on other animals. Furthermore, there is growing evidence that dogs have developed unique communication and social bonding abilities with humans, which has implications for understanding the evolution of cooperation and communication— key components of human evolutionary history. Through their domestication, dogs may have undergone an evolutionary convergence with humans, adapting to similar environmental conditions, which makes them an insightful model for exploring human evolution. Beyond evolutionary studies, dogs can also serve as important models for understanding human health. Companion dogs live in human homes around the world and are exposed to many of the same environmental factors as their human counterparts, such as diet, exercise, pathogens, and chemicals. This offers unique opportunities to study health outcomes in a real-world context, which is often difficult to achieve using laboratory organisms. Ethically, anthropologists working with dogs should follow guidelines similar to those used in research involving human infants and children. This would ensure that the treatment of dogs in research is humane, with an emphasis on minimizing harm and respecting their well-being. Additionally, researchers should aim to study dogs from a diverse range of environments and cultural contexts to fully appreciate the diversity of both canine and human experiences. This approach will help uncover the broad range of factors that influence health, behavior, and evolution in both species.

References

Albuquerque, N., Guo, K., Wilkinson, A., Savalli, C., Otta, E., & Mills, D. (2016). Dogs recognize dog and human emotions. *Biology Letters*, *12*(1), 1–5. https://doi.org/10.1098/rsbl.2015.0883

Ameen, C., Feuerborn, T. R., Brown, S. K., Linderholm, A., Hulme-Beaman, A., Lebrasseur, O., Sinding, M. H. S., Lounsberry, Z. T., Lin, A. T., Appelt, M., Bachmann, L., Betts, M., Britton, K., Darwent, J., Dietz, R., Fredholm, M., Gopalakrishnan, S., Goriunova, O. I., Grønnow, B., … Evin, A. (2019). Specialized sledge dogs accompanied Inuit dispersal across the North American Arctic. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1916). https://doi.org/10.1098/rspb.2019.1929

Anza-Burgess, K., Lepofsky, D., & Yang, D. (2020). “A part of the people”: human-dog relationships among the Northern Coast Salish of SW British Columbia. *Journal of Ethnobiology*, *40*(4), 434–450. https://doi.org/10.2993/0278-0771-40.4.434

Axelsson, E., Ratnakumar, A., Arendt, M. L., Maqbool, K., Webster, M. T., Perloski, M., Liberg, O., Arnemo, J. M., Hedhammar, Å., & Lindblad-Toh, K. (2013). The genomic signature of dog domestication reveals adaptation to a starch-rich diet. *Nature*, *495*(7441), 360–364. https://doi.org/10.1038/nature11837

Ballard, J. W. O., & Wilson, L. A. B. (2019). The Australian dingo: untamed or feral? *Frontiers in Zoology*, *16*(1), 1–19. https://doi.org/10.1186/s12983-019-0300-6

Balme, J., & O’Connor, S. (2016). Dingoes and Aboriginal social organization in Holocene Australia. *Journal of Archaeological Science: Reports*, *7*, 775–781. https://doi.org/10.1016/j.jasrep.2015.08.015

Balme, J., O’Connor, S., & Fallon, S. (2018). New dates on dingo bones from Madura Cave provide oldest firm evidence for arrival of the species in Australia. *Scientific Reports*, *8*(1), 4–9. https://doi.org/10.1038/s41598-018-28324-x

Banerjee, A., & Bhadra, A. (2021). Time-activity budget of urban-adapted free-ranging dogs. *Acta Ethologica*, *0123456789*. https://doi.org/10.1007/s10211-021-00379-6

Bastos, A. P. M., & Rossano, F. (2023). Soundboard-using pets?: Introducing a new global citizen science approach to interspecies communication. *Interaction Studies*, *24*(2), 311–334. https://www.jbe-platform.com/content/journals/10.1075/is.22050.pin

Becher, H., & Schütze, F. (1960). The Surara and Pakidai, two Yanoama tribes in northwest Brazil. In *Mitteilungen* (Vol. 26, p. 186). Kommissionsverlag Cram, De Gruyter & Co. https://ehrafworldcultures-yale-edu.ezaccess.libraries.psu.edu/document?id=sq18-002

Bentosela, M., Wynne, C. D. L., D'Orazio, M., Elgier, A., & Udell, M. A. R. (2016). Sociability and gazing toward humans in dogs and wolves: simple behaviors with broad implications. *Journal of the Experimental Analysis of Behavior*, *105*(1), 68–75. https://doi.org/10.1002/jeab.191

Bergström, A., Frantz, L., Schmidt, R., Ersmark, E., Lebrasseur, O., Girdland-Flink, L., Lin, A. T., Storå, J., Sjögren, K.-G., Anthony, D., Antipina, E., Amiri, S., Bar-Oz, G., Bazaliiskii, V. I., Bulatović, J., Brown, D., Carmagnini, A., Davy, T., Fedorov, S., … Skoglund, P. (2020). Origins and genetic legacy of prehistoric dogs. *Science*, *370*(557–564), 1–7.

Best, E. (1924). *The Maori: volume 1*. H. H. Tombs, Limited. https://ehrafworldcultures-yale-edu.ezaccess.libraries.psu.edu/document?id=oz04-001

Black, L. (1973). The Nivkh (Gilyak) of Sakhalin and the Lower Amur. *Arctic Anthropology*, *10*(1), 21–23.

Boonstra, R. (2013). Reality as the leading cause of stress: rethinking the impact of chronic stress in nature. *Functional Ecology*, *27*(1), 11–23. https://doi.org/10.1111/1365-2435.12008

Brooks, J., Kays, R., & Hare, B. (2020). Coyotes living near cities are bolder: implications for dog evolution and human-wildlife conflict. *Behaviour*, 1–25. https://doi.org/10.1163/1568539x-bja10002

Cagan, A., & Blass, T. (2016). Identification of genomic variants putatively targeted by selection during dog domestication. *BMC Evolutionary Biology*, *16*(1), 1–13. https://doi.org/10.1186/s12862-015-0579-7

Caragiulo, A., Gaughran, S. J., Duncan, N., Nagy, C., Weckel, M., & VonHoldt, B. M. (2022). Coyotes in New York City carry variable genomic dog ancestry and influence their interactions with humans. *Genes*, *13*(9). https://doi.org/10.3390/genes13091661

Chambers, J., Quinlan, M. B., Evans, A., & Quinlan, R. J. (2020). Dog-human coevolution: cross-cultural analysis of multiple hypotheses. *Journal of Ethnobiology*, *40*(4), 414–433. https://doi.org/10.2993/0278-0771-40.4.414

Chetty, R., Stepner, M., Abraham, S., Lin, S., Scuderi, B., Turner, N., Bergeron, A., & Cutler, D. (2016). The association between income and life expectancy in the United States, 2001–2014. *JAMA*, *315*(16), 1750–1766. https://doi.org/10.1001/jama.2016.4226.The

Cieri, R. L., Churchill, S. E., Franciscus, R. G., Tan, J., & Hare, B. (2014). Craniofacial feminization, social tolerance, and the origins of behavioral modernity. *Current Anthropology*, *55*(4), 419–443. https://doi.org/10.1086/677209

Cipriani, L. (1966). *The Andaman Islanders* (D. T. Cox & L. Cole, Eds.). Frederick A. Praeger, Inc. https://ehrafworldcultures-yale-edu.ezaccess.libraries.psu.edu/document?id=az02-011.%0A

Ciuti, S., Muhly, T. B., Paton, D. G., McDevitt, A. D., Musiani, M., & Boyce, M. S. (2012). Human selection of elk behavioural traits in a landscape of fear. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1746), 4407–4416. https://doi.org/10.1098/rspb.2012.1483

Cobo, B. (1893). *History of the New World* (M. J. de la Espada & A. Brunel, Eds.). Imp. de E. Rasco. https://ehrafworldcultures-yale-edu.ezaccess.libraries.psu.edu/document?id=se13-004.

Coppinger, L., & Coppinger, R. (2000). Dogs for herding and guarding livestock. In T. Grandin (Ed.), *Livestock Handling and Transport* (2nd ed., pp. 235–253).

Cunningham, P., Shankar, M., VonHoldt, B., Brzeski, K. E., & Kienle, S. S. (2024). Coyotes can do 'puppy dog eyes' too: Comparing interspecific variation in Canis facial expression muscles. *Royal Society Open Science*.

Darwin, C. (1859). *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*.

Darwin, C. (1868). *The variation of animals and plants under domestication*.

De Coccola, R., King, P., & Houston, J. (1986). *The incredible Eskimo: life among the Barren Land Eskimo*. Hancock House. https://ehrafworldcultures-yale-edu.ezaccess.libraries.psu.edu/document?id=nd08-035

Descola, P. (2013). *Beyond nature and culture*. University of Chicago Press.

D’Huy, J. (2022). De l’origine du chien et de sa diffusion à l’aune de sa mythologie à l’aune de sa mythologie. *Anthropozoologica*, *57*(7), 169–184.

D’Huy, J., Le Quellec, J. L., Thuillard, M., Berezkin, Y. E., Lajoye, P., & Oda, J. (2023). Little statisticians in the forest of tales: towards a new comparative mythology. *Fabula*, *64*(1–2), 44–63. https://doi.org/10.1515/fabula-2023-0013

Douglass, K., Gaffney, D., Feo, T. J., Bulathsinhala, P., Mack, A. L., Spitzer, M., & Summerhayes, G. R. (2021). Late Pleistocene/Early Holocene sites in the montane forests of New Guinea yield early record of cassowary hunting and egg harvesting. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(40), 1–10. https://doi.org/10.1073/pnas.2100117118

Dreschel, N. A. (2010). The effects of fear and anxiety on health and lifespan in pet dogs. *Applied Animal Behaviour Science*, *125*(3–4), 157–162. https://doi.org/10.1016/j.applanim.2010.04.003

Durán, D. (1975). *Book of the gods and rites and the ancient calendar* (F. Horcasitas, D. Heyden, & M. León-Portilla, Eds.). University of Oklahoma Press. https://ehrafworldcultures-yale-edu.ezaccess.libraries.psu.edu/cultures/nu07/documents/022

Edwards, R. W., Jeske, R. J., & Coltrain, J. B. (2017). Preliminary evidence for the efficacy of the Canine Surrogacy Approach in the Great Lakes. *Journal of Archaeological Science: Reports*, *13*(February), 516–525. https://doi.org/10.1016/j.jasrep.2017.05.008

Evershed, R. P., Smith, G. D., Roffet-Salque, M., Timpson, A., Diekmann, Y., Lyon, M. S., Cramp, L. J. E., Casanova, E., Smyth, J., Whelton, H. L., Dunne, J., Brychova, V., Šoberl, L., Gerbault, P., Gillis, R. E., Heyd, V., Johnson, E., Kendall, I., Manning, K., … Thomas, M. G. (2022). Dairying, diseases and the evolution of lactase persistence in Europe. *Nature*, *608*(7922), 336–345.

Ferrars, M., & Ferrars, B. (1901). *Burma*. Sampson Low, Marston and Company. https://ehrafworldcultures-yale-edu.ezaccess.libraries.psu.edu/document?id=ap04-025.

Fillios, M. A., & Taçon, P. S. C. (2016). Who let the dogs in? A review of the recent genetic evidence for the introduction of the dingo to Australia and implications for the movement of people. *Journal of Archaeological Science: Reports*, *7*, 782–792. https://doi.org/10.1016/j.jasrep.2016.03.001

Freedman, A. H., & Wayne, R. K. (2017). Deciphering the origin of dogs: from fossils to genomes. *Annual Review of Animal Biosciences*, *5*(1), 281–307. https://doi.org/10.1146/annurev-animal-022114-110937

Fuentes, A. (2006). The humanity of animals and the animality of humans: A view from biological anthropology inspired by J. M. Coetzee's Elizabeth Costello. *American Anthropologist*, *108*(1), 124–132. https://doi.org/10.1525/aa.2006.108.1.124

Gancz, A. S., & Weyrich, L. S. (2023). Studying ancient human oral microbiomes could yield insights into the evolutionary history of noncommunicable diseases. *F1000Research*, *12*, 109. https://doi.org/10.12688/f1000research.129036.1

Garner, J. P. (2014). The significance of meaning: Why do over 90% of behavioral neuroscience results fail to translate to humans, and what can we do to fix it? *ILAR Journal*, *55*(3), 438–456. https://doi.org/10.1093/ilar/ilu047

Goodrich, J. K., Davenport, E. R., Clark, A. G., & Ley, R. E. (2017). The relationship between the human genome and microbiome comes into view. *Annual Review of Genetics*, *51*, 413–433. https://doi.org/10.1146/annurev-genet-110711-155532

Gottelli, D., Sillero-Zubiri, C., Applebaum, G. D., Roy, M. S., Girman, D. J., Garcia-Moreno, J., Ostrander, E. A., & Wayne, R. K. (1994). Molecular genetics of the most endangered canid: the Ethiopian wolf Canis simensis. *Molecular Ecology*, *3*(4), 301–312. https://doi.org/10.1111/j.1365-294X.1994.tb00070.x

Gourou, P. (1936). *The peasants of the Tonkin delta: a study in human geography* (R. R. Miller, Ed.). Les éditions d'Art et d'Histoire. https://ehrafworldcultures-yale-edu.ezaccess.libraries.psu.edu/cultures/am11/documents/001

Greig, K., Boocock, J., Allen, M. S., Matisoo-Smith, L., & Walter, R. (2018). Ancient DNA evidence for the introduction and dispersal of dogs (Canis familiaris) in New Zealand. *Journal of Pacific Archaeology*, *9*(1), 1–10.

Grigson, W. V., & Elwin, V. (1949). *The Maria Gonds of Bastar*. Oxford University Press. https://ehrafworldcultures-yale-edu.ezaccess.libraries.psu.edu/document?id=aw32-001

Guagnin, M., Perri, A. R., & Petraglia, M. D. (2018). Pre-Neolithic evidence for dog-assisted hunting strategies in Arabia. *Journal of Anthropological Archaeology*, *49*(November 2017), 225–236. https://doi.org/10.1016/j.jaa.2017.10.003

Guiry, E. J. (2012). Dogs as analogs in stable isotope-based human paleodietary reconstructions: a review and considerations for future use. *Journal of Archaeological Method and Theory*, *19*(3), 351–376. https://doi.org/10.1007/s10816-011-9118-z

Guiry, E. J. (2013). A canine surrogacy approach to human paleodietary bone chemistry: Past development and future directions. *Archaeological and Anthropological Sciences*, *5*(3), 275–286. https://doi.org/10.1007/s12520-013-0133-8

Guy, M. K., Page, R. L., Jensen, W. A., Olson, P. N., David Haworth, J., Searfoss, E. E., & Brown, D. E. (2015). The Golden Retriever Lifetime Study: establishing an observational cohort study with translational relevance for human health. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *370*(1673). https://doi.org/10.1098/rstb.2014.0230

Hall, N. J., Johnston, A. M., Bray, E. E., Otto, C. M., MacLean, E. L., & Udell, M. A. R. (2021). Working dog training for the twenty-first century. *Frontiers in Veterinary Science*, *8*(July), 1–18. https://doi.org/10.3389/fvets.2021.646022

Hare, B. (2017). Survival of the friendliest: Homo sapiens evolved via selection for prosociality. *Annual Review of Psychology*, *68*(1), 155–186. https://doi.org/10.1146/annurev-psych-010416-044201

Hare, B., Brown, M., Williamson, C., & Tomasello, M. (2002). The domestication of social cognition in dogs. *Science*, *298*(5598), 1634–1636. https://doi.org/10.1126/science.1072702

Hare, B., Plyusnina, I., Ignacio, N., Schepina, O., Stepika, A., Wrangham, R., & Trut, L. (2005). Social cognitive evolution in captive foxes is a correlated by-product of experimental domestication. *Current Biology*, *15*, 226–230. https://doi.org/10.1016/j

Harkin, M. E. (2010). Uncommon ground: holism and the future of anthropology. *Reviews in Anthropology*, *39*(1), 25–45. https://doi.org/10.1080/00938150903548600

Hawkes, K., O'Connell, J., & Blurton Jones, N. (2018). Hunter-gatherer studies and human evolution: a very selective review. *American Journal of Physical Anthropology*, *165*(4), 777–800. https://doi.org/10.1002/ajpa.23403

Henrich, J., Heine, S. J., & Norenzayan, A. (2010). Most people are not WEIRD. *Behavioral and Brain Sciences*, *33*(2–3), 61–83. https://doi.org/10.1017/S0140525X0999152X

Herrmann, E., Call, J., Hernández-Lloreda, M. V., Hare, B., & Tomasello, M. (2007). Humans have evolved specialized skills of social cognition: The cultural intelligence hypothesis. *Science*, *317*(5843), 1360–1366. https://doi.org/10.1126/science.1146282

Hoffman, J. M., Creevy, K. E., Franks, A., O'Neill, D. G., & Promislow, D. E. L. (2018). The companion dog as a model for human aging and mortality. *Aging Cell*, *17*(3). https://doi.org/10.1111/acel.12737

Hole, F., & Wyllie, C. (2007). The oldest depictions of canines and a possible early breed of dog in Iran. *Paléorient*, *33*(1), 175–185. https://doi.org/10.3406/paleo.2007.5213

Hou, K., Wu, Z. X., Chen, X. Y., Wang, J. Q., Zhang, D., Xiao, C., Zhu, D., Koya, J. B., Wei, L., Li, J., & Chen, Z. S. (2022). Microbiota in health and diseases. *Signal Transduction and Targeted Therapy*, *7*(1). https://doi.org/10.1038/s41392-022-00974-4

Huerta-Sánchez, E., Jin, X., Asan, Bianba, Z., Peter, B. M., Vinckenbosch, N., Liang, Y., Yi, X., He, M., Somel, M., Ni, P., Wang, B., Ou, X., Huasang, Luosang, J., Cuo, Z. X. P., Li, K., Gao, G., Yin, Y., … Nielsen, R. (2014). Altitude adaptation in Tibetans caused by introgression of Denisovan-like DNA. *Nature*, *512*(7513), 194–197. https://doi.org/10.1038/nature13408

Humphrey, N. (2024). Working like a dog: canine labour, technological unemployment, and extinction in industrialising England. *Environment and History*, *30*(1), 27–52. https://doi.org/10.3197/096734022X16384451127401

Janes, C. R., & Corbett, K. K. (2009). Anthropology and global health. *Annual Review of Anthropology*, *38*, 167–183. https://doi.org/10.1146/annurev-anthro-091908-164314

Janssens, L., Giemsch, L., Schmitz, R., Street, M., Van Dongen, S., & Crombé, P. (2018). A new look at an old dog: Bonn-Oberkassel reconsidered. *Journal of Archaeological Science*, *92*, 126–138. https://doi.org/10.1016/j.jas.2018.01.004

Johnston, A. M., Turrin, C., Watson, L., Arre, A. M., & Santos, L. R. (2017). Uncovering the origins of dog–human eye contact: dingoes establish eye contact more than wolves, but less than dogs. *Animal Behaviour*, *133*, 123–129. https://doi.org/10.1016/j.anbehav.2017.09.002

Jones, R. (1970). Tasmanian Aborigines and dogs. *Mankind*, *7*(4), 256–271. https://doi.org/10.1111/j.1835-9310.1970.tb00420.x

Julian, C. G., & Moore, L. G. (2019). Human genetic adaptation to high altitude: evidence from the Andes. *Genes*, *10*(2). https://doi.org/10.3390/genes10020150

Kaeberlein, M., Creevy, K. E., & Promislow, D. E. L. (2016). The Dog Aging Project: translational geroscience in companion animals. *Mammalian Genome*, *27*(7–8), 279–288. https://doi.org/10.1007/s00335-016-9638-7.The

Kaminski, J., Waller, B. M., Diogo, R., Hartstone-Rose, A., & Burrows, A. M. (2019). Evolution of facial muscle anatomy in dogs. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(29), 14677–14681. https://doi.org/10.1073/pnas.1820653116

Koster, J. (2008). Hunting with dogs in Nicaragua: an optimal foraging approach. *Current Anthropology*, *49*(5), 935–944. https://doi.org/10.1086/592021

Koster, J. (2021). Most Dogs Are Not NATIVE Dogs. *Integrative and Comparative Biology*, *61*(1), 110–116. https://doi.org/10.1093/icb/icab016

Koungoulos, L., & Fillios, M. (2020). Hunting dogs down under? On the Aboriginal use of tame dingoes in dietary game acquisition and its relevance to Australian prehistory. *Journal of Anthropological Archaeology*, *58*(September 2019), 101146. https://doi.org/10.1016/j.jaa.2020.101146

Lane, K. S. (1952). The Montagnais Indians, 1600-1640. *The Kroeber Anthropological Society Papers*, *7*, 45.

Larson, G., Karlsson, E. K., Perri, A., Webster, M. T., Ho, S. Y. W., Peters, J., Stahl, P. W., Piper, P. J., Lingaas, F., Fredholm, M., Comstock, K. E., Modiano, J. F., Schelling, C., Agoulnik, A. I., Leegwater, P. A., Dobney, K., Vigne, J. D., Vilà, C., Andersson, L., & Lindblad-Toh, K. (2012). Rethinking dog domestication by integrating genetics, archeology, and biogeography. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(23), 8878–8883. https://doi.org/10.1073/pnas.1203005109

Lin, A. T., Hammond-Kaarremaa, L., Liu, H.-L., Stantis, C., McKechnie, I., Pavel, M., Pavel, S. S. M., Wyss, S. S., Sparrow, D. Q., Carr, K., Aninta, S. G., Perri, A., Hartt, J., Bergström, A., Carmagnini, A., Charlton, S., Dalén, L., Feuerborn, T. R., France, C. A. M., … Kistler, L. (2023). The history of Coast Salish "woolly dogs" revealed by ancient genomics and Indigenous Knowledge. *Science*, *382*(6676), 1303–1309. https://doi.org/10.1126/science.adi6549

Link, B. G., & Phelan, J. (1995). Social conditions as fundamental causes of health inequalities. *Journal of Health and Social Behavior*, *35*, 80–94. https://doi.org/10.2307/j.ctv16h2n9s.4

Liu, Y. H., Wang, L., Zhang, Z., Otecko, N. O., Khederzadeh, S., Dai, Y., Liang, B., Wang, G. D., & Zhang, Y. P. (2021). Whole-genome sequencing reveals lactase persistence adaptation in European dogs. *Molecular Biology and Evolution*, *38*(11), 4884–4890. https://doi.org/10.1093/molbev/msab214

Liu, Y.-H., Wang, L., Xu, T., Guo, X., Li, Y., Yin, T.-T., Yang, H.-C., Hu, Y., Adeola, A. C., Sanke, O. J., Otecko, N. O., Wang, M., Ma, Y., Charles, O. S., Sinding, M.-H. S., Gopalakrishnan, S., Samaniego, J. A., Hansen, A. J., Fernandes, C., … Zhang, Y.-P. (2018). Whole-genome sequencing of African dogs provides insights into adaptations against tropical parasites. *Molecular Biology and Evolution*, *35*(2), 287–298. https://doi.org/10.1093/molbev/msx258

Lupo, K. D. (2017). When and where do dogs improve hunting productivity? The empirical record and some implications for early Upper Paleolithic prey acquisition. *Journal of Anthropological Archaeology*, *47*, 139–151. https://doi.org/10.1016/j.jaa.2017.05.003

Lupo, K. D. (2019). Hounds follow those who feed them: What can the ethnographic record of hunter-gatherers reveal about early human-canid partnerships? *Journal of Anthropological Archaeology*, *55*(April), 101081. https://doi.org/10.1016/j.jaa.2019.101081

MacHugh, D. E., Larson, G., & Orlando, L. (2017). Taming the past: ancient DNA and the study of animal domestication. *Annual Review of Animal Biosciences*, *5*(1), 329–351. https://doi.org/10.1146/annurev-animal-022516-022747

MacLean, E. L., & Hare, B. (2018). Enhanced selection of assistance and explosive detection dogs using cognitive measures. *Frontiers in Veterinary Science*, *5*(236), 1–14. https://doi.org/10.3389/fvets.2018.00236

MacLean, E. L., Herrmann, E., Suchindran, S., & Hare, B. (2017). Individual differences in cooperative communicative skills are more similar between dogs and humans than chimpanzees. *Animal Behaviour*, *126*, 41–51. https://doi.org/10.1016/j.anbehav.2017.01.005

Man, E. H. (1932). *On the aboriginal inhabitants of the Andaman Islands*. The Royal Anthropological Institute of Great Britain and Ireland. https://ehrafworldcultures-yale-edu.ezaccess.libraries.psu.edu/document?id=az02-002

Marciniak, S., & Perry, G. H. (2017). Harnessing ancient genomes to study the history of human adaptation. *Nature Reviews Genetics*, *18*(11), 659–674. https://doi.org/10.1038/nrg.2017.65

Marshall-Pescini, S., Schwarz, J. F. L., Kostelnik, I., Virányi, Z., & Range, F. (2017). Importance of a species' socioecology: wolves outperform dogs in a conspecific cooperation task. *Proceedings of the National Academy of Sciences*, 201709027. https://doi.org/10.1073/pnas.1709027114

Martinez, K. B., Leone, V., & Chang, E. B. (2017). Microbial metabolites in health and disease: navigating the unknown in search of function. *Journal of Biological Chemistry*, *292*(21), 8553–8559. https://doi.org/10.1074/jbc.R116.752899

Marwaha, K., Cain, R., Asmis, K., Czaplinski, K., Holland, N., Mayer, D. C. G., & Chacon, J. (2025). Exploring the complex relationship between psychosocial stress and the gut microbiome: implications for inflammation and immune modulation. *Journal of Applied Physiology (Bethesda, Md. : 1985)*, *138*(2), 518–535. https://doi.org/10.1152/japplphysiol.00652.2024

McCoy, B. M., Brassington, L., Jin, K., Dolby, G. A., Shrager, S., Collins, D., Dunbar, M., Ruple, A., & Snyder-Mackler, N. (2023). Social determinants of health and disease in companion dogs: a cohort study from the Dog Aging Project. *Evolution, Medicine and Public Health*, *11*(1), 187–201. https://doi.org/10.1093/emph/eoad011

Meadows, J. R. S., Kidd, J. M., Wang, G. D., Parker, H. G., Schall, P. Z., Bianchi, M., Christmas, M. J., Bougiouri, K., Buckley, R. M., Hitte, C., Nguyen, A. K., Wang, C., Jagannathan, V., Niskanen, J. E., Frantz, L. A. F., Arumilli, M., Hundi, S., Lindblad-Toh, K., Ginja, C., …

Ostrander, E. A. (2023). Genome sequencing of 2000 canids by the Dog10K consortium advances the understanding of demography, genome function and architecture. *Genome Biology*, *24*(1). https://doi.org/10.1186/s13059-023-03023-7

Meggitt, M. (1965). The association between Australian Aborigines and dingoes. *Man, Culture, and Animals*, 7–26.

Miao, B., Wang, Z., & Li, Y. (2017). Genomic analysis reveals hypoxia adaptation in the Tibetan Mastiff by introgression of the gray wolf from the Tibetan Plateau. *Molecular Biology and Evolution*, *34*(3), 734–743. https://doi.org/10.1093/molbev/msw274

Miklósi, Á., Kubinyi, E., Topál, J., Gácsi, M., Virányi, Z., & Csányi, V. (2003). A simple reason for a big difference: Wolves do not look back at humans, but dogs do. *Current Biology*, *13*(13), 763–766. https://doi.org/10.1016/S

Mooney, J. A., Marsden, C. D., Yohannes, A., Wayne, R. K., & Lohmueller, K. E. (2023). Long-term small population size, deleterious variation, and altitude adaptation in the Ethiopian wolf, a severely endangered canid. *Molecular Biology and Evolution*, *40*(1), 1–14. https://doi.org/10.1093/molbev/msac277

Morey, D. F. (2006). Burying key evidence: The social bond between dogs and people. *Journal of Archaeological Science*, *33*(2), 158–175. https://doi.org/10.1016/j.jas.2005.07.009

Murray, C. (2008). The use and abuse of dogs on Scott's and Amundsen's South Pole expeditions. *Polar Record*, *44*(4), 303–310. https://doi.org/10.1017/S0032247408007493

Musharbash, Y. (2017). Telling Warlpiri dog stories. *Anthropological Forum*, *27*(2), 95–113. https://doi.org/10.1080/00664677.2017.1303603

National Commission for the Protection of Human Subjects of Biomedical and Behavioral Research. (1979). *The Belmont Report*. https://doi.org/10.1021/bi00780a005

National Research Council. (2011). *Guide for the care and use of laboratory animals* (8th ed.). National Academies Press. https://doi.org/10.17226/12910

Nelson, A. (2017). What the dogs did: animal agency in the Soviet manned space flight programme. *BJHS Themes*, *2*, 79–99. https://doi.org/10.1017/bjt.2017.9

Norton, H. L., Quillen, E. E., Bigham, A. W., Pearson, L. N., & Dunsworth, H. (2019). Human races are not like dog breeds: Refuting a racist analogy. *Evolution: Education and Outreach*, *12*(1), 1–20. https://doi.org/10.1186/s12052-019-0109-y

Nunn, C. L. (2011). *The comparative approach in evolutionary anthropology and biology*. University of Chicago Press.

Nunn, C. L., Craft, M. E., Gillespie, T. R., Schaller, M., Kappeler, P. M., & Nunn, C. L. (2015). The sociality – health – fitness nexus: synthesis , conclusions and future directions. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *370*.

O'Connor, D. B., Thayer, J. F., & Vedhara, K. (2021). Stress and health: a review of psychobiological processes. *Annual Review of Psychology*, *72*, 663–688. https://doi.org/10.1146/annurev-psych-062520-122331

Okere, L. C. (1980). *Socio-economic and cultural aspects of food and food habits in rural Igboland*. University Microfilms. https://ehrafworldcultures-yale-edu.ezaccess.libraries.psu.edu/document?id=ff26-029

Palkovitz, R. E., & Lawler, R. R. (2024). Developing evolutionary anthropology in local ecosystems. *Evolutionary Anthropology*, *33*(1), 1–9. https://doi.org/10.1002/evan.22016

Parsons, K. J., Rigg, A., Conith, A. J., Kitchener, A. C., Harris, S., & Zhy, H. (2020). Skull morphology diverges between urban and rural populations of red foxes mirroring patterns of domestication and macroevolution. *Proceedings of the Royal Society B: Biological Sciences*, *287*.

Paul, M., Sen Majumder, S., Sau, S., Nandi, A. K., & Bhadra, A. (2016). High early life mortality in free-ranging dogs is largely influenced by humans. *Scientific Reports*, *6*(September 2015), 1–8. https://doi.org/10.1038/srep19641

Pegram, C., Gray, C., Packer, R. M. A., Richards, Y., Church, D. B., Brodbelt, D. C., & O'Neill, D. G. (2021). Proportion and risk factors for death by euthanasia in dogs in the UK. *Scientific Reports*, *11*(1), 1–12. https://doi.org/10.1038/s41598-021-88342-0

Peng, M. S., Liu, Y. H., Shen, Q. K., Zhang, X. H., Dong, J., Li, J. X., Zhao, H., Zhang, H., Zhang, X., He, Y., Shi, H., Cui, C., Ouzhuluobu, Wu, T. Y., Liu, S. M., Gonggalanzi, Baimakangzhuo, Bai, C., Duojizhuoma, … Zhang, Y. P. (2023). Genetic and cultural adaptations underlie the establishment of dairy pastoralism in the Tibetan Plateau. *BMC Biology*, *21*(1), 1–14. https://doi.org/10.1186/s12915-023-01707-x

Perri, A. R. (2016). Hunting dogs as environmental adaptations in Jōmon Japan. *Antiquity*, *90*(353), 1166–1180. https://doi.org/10.15184/aqy.2016.115

Perri, A. R. (2020). Prehistoric dogs as hunting weapons: the advent of animal biotechnology. In B. Berthke & A. Burtt (Eds.), *Dogs: Archaeology of the Human-Canine Connection Beyond Domestication* (pp. 7–44). University Press of Florida.

Perri, A. R., Feuerborn, T. R., Frantz, L. A. F., Larson, G., & Malhi, R. S. (2021). Dog domestication and the dual dispersal of people and dogs into the Americas. *Proceedings of the National Academy of Sciences*, *118*(6), 1–8. https://doi.org/10.1073/pnas.2010083118

Perri, A. R., Koster, J. M., Otárola-Castillo, E., Burns, J. L., & Cooper, C. G. (2019). Dietary variation among indigenous Nicaraguan horticulturalists and their dogs: An ethnoarchaeological application of the Canine Surrogacy Approach. *Journal of Anthropological Archaeology*, *55*(March). https://doi.org/10.1016/j.jaa.2019.05.002

Perry, G. H. (2020). How human behavior can impact the evolution of genetically-mediated behavior in wild non-human species. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, *206*(3), 337–342. https://doi.org/10.1007/s00359-020-01415-9

Perry, G. H., Dominy, N. J., Claw, K. G., Lee, A. S., Fiegler, H., Redon, R., Werner, J., Villanea, F. A., Mountain, J. L., Misra, R., Carter, N. P., Lee, C., & Stone, A. C. (2007). Diet and the evolution of human amylase gene copy number variation. *Nature Genetics*, *39*(10), 1256–1260. https://doi.org/10.1038/ng2123

Pew Research Center. (2006). Gauging family intimacy: dogs edge cats (dads trail both). In *Pew Research Center: A Social Trends Report*.

Pilley, J. W., & Reid, A. K. (2011). Border collie comprehends object names as verbal referents. *Behavioural Processes*, *86*(2), 184–195. https://doi.org/10.1016/j.beproc.2010.11.007

Pitulko, V. V., & Kasparov, A. K. (2017). Archaeological dogs from the Early Holocene Zhokhov site in the Eastern Siberian Arctic. *Journal of Archaeological Science: Reports*, *13*(May), 491–515. https://doi.org/10.1016/j.jasrep.2017.04.003

Pospisil, L. J. (1958). Kapauku Papuans and Their Law. In *Yale University Publications in Anthropology* (p. 33). Department of Anthropology, Yale University. https://ehrafworldcultures-yale-edu.ezaccess.libraries.psu.edu/document?id=oj29-001

Radcliffe-Brown, A. R. (1922). *The Andaman Islanders: a study in social anthropology*. Cambridge University Press. https://ehrafworldcultures-yale-edu.ezaccess.libraries.psu.edu/document?id=az02-001

Raswan, C. R. (1947). *Black tents of Arabia*. Creative Age Press. https://ehrafworldcultures-yale-edu.ezaccess.libraries.psu.edu/document?id=md04-001

Ravinet, M., Elgvin, T. O., Trier, C., Aliabadian, M., Gavrilov, A., & Sætre, G. P. (2018). Signatures of human-commensalism in the house sparrow genome. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1884). https://doi.org/10.1098/rspb.2018.1246

Reese, A. T., Chadaideh, K. S., Diggins, C. E., Schell, L. D., Beckel, M., Callahan, P., Ryan, R., Thompson, M. E., & Carmody, R. N. (2021). Effects of domestication on the gut microbiota parallel those of human industrialization. *ELife*, *10*, 1–27. https://doi.org/10.7554/eLife.60197

Reiter, T., Jagoda, E., & Capellini, T. D. (2016). Dietary variation and evolution of gene copy number among dog breeds. *PLoS ONE*, *11*(2), 1–19. https://doi.org/10.1371/journal.pone.0148899

Rodman, P. S. (1999). Whither primatology? The place of primates in contemporary anthropology. *Annual Review of Anthropology*, *28*(1999), 311–339.

Ross, F. C., Patangia, D., Grimaud, G., Lavelle, A., Dempsey, E. M., Ross, R. P., & Stanton, C. (2024). The interplay between diet and the gut microbiome: implications for health and disease. *Nature Reviews Microbiology*, *22*(November). https://doi.org/10.1038/s41579-024-01068-4

Ruple, A., Maclean, E., Snyder-Mackler, N., Creevy, K. E., & Promislow, D. (2022). Dog models of aging. *Annual Review of Animal Biosciences*, *10*, 419–439. https://doi.org/10.1146/annurev-animal-051021-080937

Salomons, H., Smith, K. C. M., Callahan-Beckel, M., Callahan, M., Levy, K., Kennedy, B. S., Bray, E. E., Gnanadesikan, G. E., Horschler, D. J., Gruen, M., Tan, J., White, P., VonHoldt, B. M., MacLean, E. L., & Hare, B. (2021). Cooperative communication with humans evolved to emerge early in domestic dogs. *Current Biology*, *31*(July), 1–8. https://doi.org/10.1016/j.cub.2021.06.051

Sánchez-Villagra, M. R., Geiger, M., & Schneider, R. A. (2016). The taming of the neural crest: A developmental perspective on the origins of morphological covariation in domesticated mammals. *Royal Society Open Science*, *3*(6). https://doi.org/10.1098/rsos.160107

Sánchez-Villagra, M. R., & van Schaik, C. P. (2019). Evaluating the self-domestication hypothesis of human evolution. *Evolutionary Anthropology*, *28*(3), 133–143. https://doi.org/10.1002/evan.21777

Sapolsky, R. M. (2004). Social status and health in humans and other animals. *Annual Review of Anthropology*, *33*(1), 393–418. https://doi.org/10.1146/annurev.anthro.33.070203.144000

Savage, J. (2012, December 27). Dogs and cats "still eaten in Switzerland." *The Local*. https://www.thelocal.ch/20121227/dogs-still-eaten-in-switzerland

Scheinfeldt, L. B., Soi, S., Thompson, S., Ranciaro, A., Woldemeskel, D., Beggs, W., Lambert, C., Jarvis, J. P., Abate, D., Belay, G., & Tishkoff, S. A. (2012). Genetic adaptation to high altitude in the Ethiopian highlands. *Genome Biology*, *13*(1), R1. https://doi.org/10.1186/gb-2012-13-1-r1

Ségurel, L., & Bon, C. (2017). On the evolution of lactase persistence in humans. *Annual Review of Genomics and Human Genetics*, *18*(April), 297–319. https://doi.org/10.1146/annurev-genom-091416-035340

Segurel, L., Guarino-Vignon, P., Marchi, N., Lafosse, S., Laurent, R., Bon, C., Fabre, A., Hegay, T., & Heyer, E. (2020). Why and when was lactase persistence selected for? Insights from Central Asian herders and ancient DNA. *PLoS Biology*, *18*(6), 1–11. https://doi.org/10.1371/journal.pbio.3000742

Serpell, J. A. (2021). Commensalism or cross-species adoption? A critical review of theories of wolf domestication. *Frontiers in Veterinary Science*, *8*(April), 1–10. https://doi.org/10.3389/fvets.2021.662370

Shannon, L. M., Boyko, R. H., Castelhano, M., Corey, E., Hayward, J. J., McLean, C., White, M. E., Said, M. A., Anita, B. A., Bondjengo, N. I., Calero, J., Galov, A., Hedimbi, M., Imam, B., Khalap, R., Lally, D., Masta, A., Oliveira, K. C., Pérez, L., … Boyko, A. R. (2015). Genetic structure in village dogs reveals a Central Asian domestication origin. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(44), 13639–13644. https://doi.org/10.1073/pnas.1516215112

Shipman, P. (2020). What the dingo says about dog domestication. *The Anatomical Record*, *December 2019*, 1–12. https://doi.org/10.1002/ar.24517

Smith, B. P., & Litchfield, C. A. (2009). A review of the relationship between indigenous Australians, dingoes (Canis dingo) and domestic dogs (Canis familiaris). *Anthrozoös*, *22*(2), 111–128. https://doi.org/10.2752/175303709X434149

Smith, B. P., & Litchfield, C. A. (2013). Looking back at "looking back": operationalising referential gaze for dingoes in an unsolvable task. *Animal Cognition*, *16*(6), 961–971. https://doi.org/10.1007/s10071-013-0629-8

Snyder-Mackler, N., Burger, J. R., Gaydosh, L., Belsky, D. W., Noppert, G. A., Campos, F. A., Bartolomucci, A., Yang, Y. C., Aiello, A. E., O'Rand, A., Harris, K. M., Shively, C. A., Alberts, S. C., & Tung, J. (2020). Social determinants of health and survival in humans and other animals. *Science*, *368*(6493), eaax9553. https://doi.org/10.1126/science.aax9553

Snyder-Mackler, N., Sanz, J., Kohn, J. N., Brinkworth, J. F., Morrow, S., Shaver, A. O., Grenier, J. C., Pique-Regi, R., Johnson, Z. P., Wilson, M. E., Barreiro, L. B., & Tung, J. (2016). Social status alters immune regulation and response to infection in macaques. *Science*, *354*(6315), 1041–1045. https://doi.org/10.1126/science.aah3580

Song, S. J., Lauber, C., Costello, E. K., Lozupone, C. A., Humphrey, G., Berg-Lyons, D., Gregory Caporaso, J., Knights, D., Clemente, J. C., Nakielny, S., Gordon, J. I., Fierer, N., & Knight, R. (2013). Cohabiting family members share microbiota with one another and with their dogs. *ELife*, *2013*(2), 1–22. https://doi.org/10.7554/eLife.00458

Stewart, L., MacLean, E. L., Ivy, D., Woods, V., Cohen, E., Rodriguez, K., McIntyre, M., Mukherjee, S., Call, J., Kaminski, J., Miklósi, Á., Wrangham, R. W., & Hare, B. (2015). Citizen science as a new tool in dog cognition research. *PLoS ONE*, *10*(9), 1–16. https://doi.org/10.1371/journal.pone.0135176

Sullivan, A. P., Bird, D. W., & Perry, G. H. (2017). Human behaviour as a long-term ecological driver of non-human evolution. *Nature Ecology and Evolution*, *1*(3), 1–11. https://doi.org/10.1038/s41559-016-0065

Tanaka, J. (1976). Subsistence ecology of central Kalahari San. In *Kalahari Hunter-Gatherers : Studies of the !Kung San and Their Neighbors* (p. 112). Harvard University Press. https://ehrafworldcultures-yale-edu.ezaccess.libraries.psu.edu/document?id=fx10-046

Thalmann, O., Shapiro, B., Cui, P., Schuenemann, V. J., Sawyer, S. K., Greenfield, D. L., Germonpré, M. B., Sablin, M. V., López-Giráldez, F., Domingo-Roura, X., Napierala, H., Uerpmann, H.-P., Loponte, D. M., Acosta, A. A., Giemsch, L., Schmitz, R. W., Worthington, B., Buikstra, J. E., Druzhkova, A., … Wayne, R. K. (2013). Complete mitochondrial genomes of ancient canids suggest a European origin of domestic dogs. *Science*, *342*(November), 871–874.

Theofanopoulou, C., Gastaldon, S., O'Rourke, T., Samuels, B. D., Messner, A., Martins, P. T., Delogu, F., Alamri, S., & Boeckx, C. (2017). Self-domestication in Homo sapiens: insights from comparative genomics. *PLoS ONE*, *12*(10), 5–7. https://doi.org/10.1371/journal.pone.0185306

Trut, L. (1999). Early canid domestication: The farm-fox experiment. *American Scientist*, *87*(2), 160. https://doi.org/10.1511/1999.20.813

Trut, L., Oskina, I., & Kharlamova, A. (2009). Animal evolution during domestication: the domesticated fox as a model. *Bioessays*, *31*(3), 349–360. https://doi.org/10.1038/jid.2014.371

Trut, L., Plyusnina, I. Z., & Oskina, I. N. (2004). An experiment on fox domestication and debatable issues of evolution of the dog. *Russian Journal of Genetics*, *40*(6), 644–655.

Vanhooren, V., & Libert, C. (2013). The mouse as a model organism in aging research: Usefulness, pitfalls and possibilities. *Ageing Research Reviews*, *12*(1), 8–21. https://doi.org/10.1016/j.arr.2012.03.010

Vilà, C., Savolainen, P., Maldonado, J. E., Amorim, I. R., Rice, J. E., Honeycutt, R. L., Crandall, K. A., Lundeberg, J., & Wayne, R. K. (1997). Multiple and ancient origins of the domestic dog. *Science*, *276*(5319), 1687–1689.

VonHoldt, B. M., Shuldiner, E., Koch, I. J., Kartzinel, R. Y., Hogan, A., Brubaker, L., Wanser, S., Stahler, D., Wynne, C. D. L., Ostrander, E. A., Sinsheimer, J. S., & Udell, M. A. R. (2017). Structural variants in genes associated with human Williams-Beuren syndrome underlie stereotypical hypersociability in domestic dogs. *Science Advances*, *3*(7). https://doi.org/10.1126/sciadv.1700398

Vorren, O., Manker, E., & McFarlane, K. (1962). *Lapp life and customs: a survey*. Oxford University Press. https://ehrafworldcultures-yale-edu.ezaccess.libraries.psu.edu/document?id=ep04-016

Waller, B. M., Peirce, K., Caeiro, C. C., Scheider, L., Burrows, A. M., McCune, S., & Kaminski, J. (2013). Paedomorphic facial expressions give dogs a selective advantage. *PLoS ONE*, *8*(12). https://doi.org/10.1371/journal.pone.0082686

Wang, G. D., Fan, R. X., Zhai, W., Liu, F., Wang, L., Zhong, L., Wu, H., Yang, H. C., Wu, S. F., Zhu, C. L., Li, Y., Gao, Y., Ge, R. L., Wu, C. I., & Zhang, Y. P. (2014). Genetic convergence in the adaptation of dogs and humans to the high-altitude environment of the Tibetan Plateau. *Genome Biology and Evolution*, *6*(8), 2122–2128. https://doi.org/10.1093/gbe/evu162

Wang, G. D., Zhai, W., Yang, H. C., Wang, L., Zhong, L., Liu, Y. H., Fan, R. X., Yin, T. T., Zhu, C. L., Poyarkov, A. D., Irwin, D. M., Hytönen, M. K., Lohi, H., Wu, C. I., Savolainen, P., & Zhang, Y. P. (2016). Out of southern East Asia: The natural history of domestic dogs across the world. *Cell Research*, *26*(1), 21–33. https://doi.org/10.1038/cr.2015.147

Welker, M. H., & Byers, D. A. (2019). The birch creek canids and dogs as transport labor in the intermountain west. *American Antiquity*, *84*(1), 88–106. https://doi.org/10.1017/aaq.2018.81

White, I. M. (1972). Hunting dogs at Yalata. *Mankind*, *8*(3), 201–205. https://doi.org/10.1111/j.1835-9310.1972.tb00436.x

Wilkins, A. S., Wrangham, R. W., & Tecumseh Fitch, W. (2014). The “domestication syndrome” in mammals: A unified explanation based on neural crest cell behavior and genetics. *Genetics*, *197*(3), 795–808. https://doi.org/10.1534/genetics.114.165423

Wood, E. K., Maddux, S. D., Southard, T. E., Kharlamova, A., Trut, L., & Franciscus, R. G. (2019). The effect of behavioral selection on the dentition of Russian silver foxes and its implications for human dental evolution. *The FASEB Journal*, *33*(1).

Wrangham, R. W. (2019). Hypotheses for the evolution of reduced reactive aggression in the context of human self-domestication. *Frontiers in Psychology*, *10*(August), 1–11. https://doi.org/10.3389/fpsyg.2019.01914

Yarlagadda, K., Zachwieja, A. J., De Flamingh, A., Phungviwatnikul, T., Rivera-Colon, A. G., Roseman, C., Shackelford, L., Swanson, K. S., & Malhi, R. S. (2022). Geographically diverse canid sampling provides novel insights into pre-industrial microbiomes. *Proceedings of the Royal Society B: Biological Sciences*, *289*(1974). https://doi.org/10.1098/rspb.2022.0052

Zeder, M. A. (2012). The domestication of animals. *Journal of Anthropological Research*, *68*(2), 161–190.

Zeder, M. A. (2017). Domestication as a model system for the extended evolutionary synthesis. *Interface Focus*, *7*(5). https://doi.org/10.1098/rsfs.2016.0133

Zhang, S., Wang, G.-D., Ma, P., Zhang, L., Yin, T.-T., Liu, Y., Otecko, N. O., Wang, M., Ma, Y., Wang, L., Mao, B., Savolainen, P., & Zhang, Y. (2020). Genomic regions under selection in the feralization of the dingoes. *Nature Communications*, *11*(1), 1–10. https://doi.org/10.1038/s41467-020-14515-6

Chapter 3

Dog Cognition Tasks Validated by Owner Surveys in Citizen Science Dataset

Introduction

Dogs are the oldest and most widely distributed domesticated animals and have historically served a diverse array of functions in human societies. The ancestors of modern dogs were domesticated from gray wolves in Eurasia during the Late Pleistocene, possibly on multiple occasions (Freedman & Wayne, 2017; Shannon et al., 2015; Thalmann et al., 2013; Vilà et al., 1997; Wang et al., 2016). Following domestication, dogs spread across Eurasia and into Africa (Bergström et al., 2020) and Australia (Balme et al., 2018; Fillios & Taçon, 2016), and they accompanied human migrations into the Americas (Perri et al., 2021), Polynesia (Greig et al., 2018), and the Arctic (Ameen et al., 2019). By the onset of Western European colonialism, which further dispersed European breeds of dogs globally (Bergström et al., 2020), only a few societies remained that did not have dogs (Cipriani, 1966; Jones, 1970; Lupo, 2017).

Dogs have long served as watchdogs and hunting companions in forager societies, likely among the oldest functional roles assigned to them in human societies (Guagnin et al., 2018; Hole & Wyllie, 2007; Perri, 2020; Serpell, 2021). Other long-standing roles include herding livestock and hauling sleds, which have existed for thousands of years across various societies (Coppinger & Coppinger, 2000; Pitulko & Kasparov, 2017). Modern working dogs continue to perform these ancient tasks while also undertaking new roles, such as assisting people with blindness, deafness, and other disabilities, as well as detecting contraband, diseases, and more (Hall et al., 2021). In various cultures, dogs have also formed close bonds with humans and are sometimes regarded as kin (Chambers et al., 2020).

It has been proposed that domestication resulted in the evolution of advanced social cognition in dogs (Hare et al., 2002; Hare & Tomasello, 2005; Salomons et al., 2021) and that dogs' cognitive abilities play an important role in determining their level of success at various working jobs (Hare & Ferrans, 2021; MacLean & Hare, 2018). Compared to even highly socialized wolves, dogs are more successful at comprehending human gestures (Hare et al., 2002; Salomons et al., 2021) and are more likely to make eye contact with humans when confronted with a task that they cannot solve without human intervention (Miklósi et al., 2003a; Salomons et al., 2021). Similarly, foxes that were experimentally domesticated over multiple generations outperformed randomly bred control-line foxes in following human gestures, indicating that domestication can shape social cognition (Hare et al., 2005). An analysis of the ethnographic record from diverse societies found that dogs were often reported to be very food stressed, and that energetically-demanding jobs like hauling and hunting were often accompanied by targeted provisioning, sometimes contingent on the dog's success that day (Lupo, 2019). This could have provided a selective advantage to traits, including cognitive abilities, that improved dogs' job performance or otherwise increased the likelihood of human-provided food. Indeed, cognitive traits, both social (e.g., gesture comprehension) and nonsocial (e.g., working memory), have been found to significantly predict the success of military detection dogs (MacLean & Hare, 2018). This evidence suggests that cooperation with humans in working contexts is closely linked to dogs' cognitive traits.

Cognition refers to the set of processes by which an organism acquires, processes, and acts on information from its environment (Shettleworth, 2010). For cognition to evolve, it must vary across individuals in ways that are at least partially heritable, and it must also affect survival and/or reproduction. Because cognition is internal to the individual, its evolutionary impact depends on how it shapes that individual's interactions with its environment. Previous work has suggested that the selective pressures of domestication have altered dogs' social cognition (Hare et al., 2002, 2005; Miklósi et al., 2003b; Salomons et al., 2021) and that the cognition of working dogs is critical for their success (Hare & Ferrans, 2021; MacLean & Hare, 2018). However, these studies have not thoroughly examined how specific cognitive abilities influence dogs' interactions with humans and their broader environment. Our ability to interpret findings from cognitive tasks depends on whether these tasks accurately measure traits that influence real-world behavior in dogs. Improving the validation of dog cognition tasks will enhance our ability to assess cognitive differences among individual dogs, between dogs that evolved to perform different functions, and between dogs and wolves. This will inform our understanding of how selection has shaped domesticated animals as well as dogs bred for different purposes.

In science, a good measurement is both reliable and valid (Martin & Bateson, 2017). A reliable measurement consistently produces the same value, whether recorded by the same observer multiple times or by different observers (Martin & Bateson, 2017). However, reliability does not ensure validity. A valid measurement accurately captures the trait it is designed to assess (Martin & Bateson, 2017). Dogs' cognition is often assessed through cognitive tasks, in which dogs make decisions in lab-based tests that reveal their internal processes (Stewart et al., 2015). Because cognition influences how an animal processes and responds to information, it should also be reflected in the animal's behavior (Shettleworth, 2010). Thus, behavioral measurements provide a potential method for externally validating dog cognition tasks. There are several ways to assess a dog's behavioral patterns. Surveys allow dog owners, who observe their dogs' behavior over time, to infer internal states (Hsu & Serpell, 2003; Miklósi, 2015). Alternatively, behavioral observations using an ethogram, a predefined list of behaviors that are systematically recorded when observed, offer a structured approach to studying behavior in both wild and domestic animals, including dogs (Miklósi, 2015).

Few studies have attempted to validate lab-based dog cognition and behavior tasks using surveys or real-world behavioral observations. In one study, semi-free ranging dogs in southern

Chile were given a laboratory test where they had the opportunity to explore an unfamiliar room, and their daily movements were tracked with GPS collars. Dogs that spent more time exploring the novel room did in fact have larger home ranges and travel farther from home, providing some validation of this test as a measure of exploratory tendencies in dogs (Saavedra-Aracena et al., 2021). In Sweden, 697 dogs were given a testing battery called the Dog Mentality Assessment, and their owners completed a behavioral questionnaire one or two years later. Results showed that the behavioral test dimensions of playfulness, curiosity/fearlessness, and sociability aligned with similar dimensions from the survey. However, a laboratory test of chase-proneness correlated with play interest but not predatory behavior, and a test of aggression showed weak correspondence with owner-reported aggression (Svartberg, 2005). Another study assessed canine frustration by exposing dogs to frustration-inducing tasks and having owners fill out the Canine Frustration Questionnaire. Frustration behaviors in the lab, such as vocalizing and lunging, correlated with scores from the questionnaire (McPeake et al., 2021). Meanwhile, studies validating laboratory tests of dog impulsivity have produced mixed results. While one found evidence of validation (Brady et al., 2018), two others did not (Mongillo et al., 2019; Stevens et al., 2022).

While these studies provide some evidence of validation for certain laboratory-based tasks measuring dog cognition and behavior, further research is needed to determine the extent to which various tasks align with survey and observational measurements. Such overlap would indicate that these tasks measure the same underlying traits, while a lack of correlation could reflect biases in measurement tools or differences in the traits being assessed. Validating cognitive tasks is especially important for those central to understanding domestication or those linked to working dog outcomes. In this study, we analyze a large citizen science dataset of cognitive tasks conducted by dog owners at home and assess their validity by comparing them to owner-completed survey responses characterizing their dogs' behavior. We hypothesize that cognitive task performance will correlate with survey measures of the same traits.

Methods

Data collection and processing

Dognition is a citizen science project in which participants conducted a cognitive task battery with their own dogs at home. The data analyzed in this study represents the Dognition data collected from 2013 to 2016. Before engaging in any cognitive tasks, owners answered 30 questions (henceforth called the pre-survey) about the dog's behavior, with some questions specifically designed to assess traits expected to correlate with cognitive tasks (Appendix A). After completing the pre-survey, participants carried out a battery of cognitive tasks intended to measure traits such as empathy, communication, perspective-taking, memory, and reasoning (Table 3-1). A previous factor analysis of the initial sample of this dataset found that these tasks clustered into principal components that the authors interpreted as representing communication, perspective-taking, memory, and empathy (Stewart et al., 2015). Following the cognitive testing, dog owners who logged back into the platform were presented with additional survey questions from a pool of over 100 (the combination of the pre-survey and these questions is henceforth referred to as the full survey; Appendix A). However, participation in these follow-up surveys varied, with substantial differences in the number of responses per question. Owners completed the pre-survey for 9,686 dogs, but subsequent task participation dropped off from there. Several past studies have used the Dognition dataset to analyze the relationship between the different cognitive tasks (Stewart et al., 2015) and to look for associations with breed (Gnanadesikan et al., 2020; Horschler et al., 2019) and age (Watowich et al., 2020), but other than a question about training history, none of the survey questions have previously been compared to the cognitive task performance.

For this analysis, we included all Dognition tasks except for the contagious yawning task, as previous studies found its effect size to be extremely small (Stewart et al., 2015). Past analyses of this dataset have used two different methods of analyzing the perspective-taking task: one measuring the average time dogs waited before eating prohibited food (Gnanadesikan et al., 2020) and the other measuring the difference in wait time when a human is watching versus not watching (Stewart et al., 2015). To determine whether these measures capture different aspects of dogs' cognition or behavior, we analyzed both.

Table **3-1**: Summary of Dognition tasks analyzed in this study.

Task	Number of Trials	Description	Question Themes Examined
Eye Contact	4	Human holds treat by eye and records duration of time for dog to break eye contact, up to 90 s.	Eye contact Empathy Food motivation Human interest
Arm Pointing	6	Human places two treats on floor, points to one with the hand, and lets dog choose.	Communication Human interest
Foot Pointing	6	Human places two treats on floor, points to one with the food, and lets dog choose.	Communication Human interest
Gaze Sensitivity to Back Turned	2 back turned, 2 observed	Human places treat on ground, forbids dog from eating it, and records duration of time for dog to consume treat, up to 90 s. Average time on two trials with dog observed are subtracted from average time on two trials with back turned.	Gaze sensitivity Human interest
Gaze Sensitivity to Eyes Closed	2 eyes covered, 2 observed	Human places treat on ground, forbids dog from eating it, and records duration of time for dog to consume treat, up to 90 s. Average time on two trials with dog observed are subtracted from average time on two trials with eyes covered with hands.	Gaze sensitivity Human interest
Latency to Eat Prohibited Food When Unobserved	2 back turned, 2 eyes covered	Human places treat on ground, forbids dog from eating it, and records duration of time for dog to consume treat, up to 90 s. Latency is the average of the two trials with back turned and two trials with eyes covered.	Eye contact Food motivation Self-control Training Gaze sensitivity
Memory vs. Pointing	6	Human places a treat under one of two cups with the dog watching, points to the incorrect cup, and lets dog choose.	Memory Communication
Memory vs. Smell	4	Human places a treat under one of two cups with the dog watching, quietly swabs the treat location while an assistant covers the dog's eyes, and lets dog choose.	Memory Smell Hearing
Memory	4	Human places a treat under one of two cups with the dog watching, waits an increasing amount of time each trial (60, 90, 120, and 180 s), and lets dog choose.	Memory
Inferential Reasoning	4	Human places a treat under one of two cups without the dog seeing where it is, lifts the empty cup to reveal that it does not have the treat, and lets dog choose.	Reasoning
Physical Reasoning	4	Human places a treat under one of two pieces of paper without the dog seeing where it is and then lets the dog choose.	Reasoning

Data analysis

To assess the extent to which owner-reported behavior aligned with cognitive task performance, we first reviewed the survey questions and generated a priori predictions about which questions would likely correlate with latent variables measured by the cognitive tasks (Appendix A). We then conducted a series of linear models to evaluate how well each survey question predicted dogs' performance on each task. Most survey questions were binary or ordinal, with an additional option for uncertainty or non-applicability. Uncertain/NA responses were removed, and all remaining answers were ordered sequentially. To facilitate comparisons of effect sizes, responses were standardized to a mean of 0 and a standard deviation of 1.

After data processing, we ran separate linear models for each Dognition cognitive task and each survey question. Binomial generalized linear models were used for tasks involving a series of binary choices, while linear models were applied to continuous outcomes. To account for multiple testing, we applied Bonferroni corrections by adjusting the $p<0.05$ significance threshold based on the number of statistical tests conducted for each task. This analysis was performed in two stages: first, using only the 30 pre-survey questions (including only dogs with complete datasets), and then again using all survey questions (with varying sample sizes per question). This two-pronged approach balances conservatism and exploration. The conservative analysis of pre-survey questions ensures higher and more comparable statistical power across questions while minimizing potential biases from owners' observations of their dogs' task performance. The exploratory analysis, which includes all survey questions, introduces potential biases from post-task responses and variable statistical power but provides a richer dataset for identifying novel associations not captured by the pre-survey alone.

Results

In the eye contact task, the dog owner held a treat by the eye and recorded how long the dog maintained eye contact, which was averaged across three trials. Survey questions hypothesized to relate to this task included those on eye contact (3 questions in both analyses), empathy (3 questions in both analyses), food motivation (1 in the pre-survey, 5 in the full survey), and human interest (1 in the pre-survey, 14 in the full survey). As expected, survey responses indicating that the dog made more eye contact were significantly associated with longer eye contact duration in both the conservative and exploratory analyses (Table 3-2, Appendix B). Questions related to empathy and food motivation also generally correlated with longer eye contact, and when significant, the associations were always in the predicted direction. In the conservative analysis, the human interest question was associated with longer eye contact as expected, but in the exploratory analysis, human interest questions showed low rates of significant associations with eye contact duration (Table 3-2, Appendix B).

Table **3-2**: Summary of questions significantly associated with eye contact task.

Conservative Analysis (*n* = 4,138)

Question Topic	Questions significant in predicted direction	Questions significant in opposite direction	Questions not significant	Total number of questions
Eye contact	3 (100%)	0 (0%)	0 (0%)	3
Empathy	2 (67%)	0 (0%)	1 (33%)	3
Food motivation	1 (100%)	0 (0%)	0 (0%)	1
Human interest	1 (100%)	0 (0%)	0 (0%)	1
Other	15 (68%)		7 (32%)	22
Total	22 (73%)		8 (27%)	30

Exploratory Analysis (*n* = 1,869 to 16,334)

Question Topic	Questions significant in predicted direction	Questions significant in opposite direction	Questions not significant	Total number of questions
Eye contact	3 (100%)	0 (0%)	0 (0%)	3
Empathy	3 (100%)	0 (0%)	0 (0%)	3
Food motivation	4 (80%)	1 (20%)	0 (0%)	5
Human interest	3 (21%)	0 (0%)	11 (79%)	14
Other	33 (32%)		71 (68%)	104
Total	47 (36%)		82 (64%)	129

In the arm pointing task, the human pointed to one of two treats, and the dog chose between them across six trials. We hypothesized that performance on this task would correlate with survey questions related to the dog's communicative abilities and interest in humans. Twelve survey questions related to communicative abilities were identified, which were present in both the pre-survey and full survey. Most of these questions were significantly associated with arm pointing performance in both the conservative and exploratory analyses. Every significant association was in the expected direction—dogs rated as more communicative by their owners were more likely to follow the pointing gesture (Table 3-3, Appendix C). Twelve questions related to human interest were identified in the full survey, two of which were also in the pre-survey. In the conservative analysis, both pre-survey questions showed stronger associations with the arm pointing task, while in the exploratory analysis, the significance rate for human interest questions was comparable to the overall rate of significant associations (Table 3-3, Appendix C). As with the communication-related questions, all significant human interest associations were in the expected direction. The foot pointing task followed the same procedure as the arm pointing task, except that the pointing gesture was made with the foot. The same survey questions were predicted to be relevant. Similar to arm pointing, communication-related questions were frequently associated with foot pointing success, while human interest questions showed more ambiguous results (Table 3-4, Appendix D). However, all significant associations for foot pointing were also in the expected direction.

Table **3-3**: Summary of questions significantly associated with arm pointing task.

Conservative Analysis (*n* = 2,877)

Question Topic	Questions significant in predicted direction	Questions significant in opposite direction	Questions not significant	Total number of questions
Communication	8 (67%)	0 (0%)	4 (33%)	12
Human interest	2 (100%)	0 (0%)	0 (0%)	2
Other	3 (19%)		13 (81%)	16
Total	13 (43 %)		17 (57%)	30

Exploratory Analysis (*n* = 1,508 to 11,376)

Question Topic	Questions significant in predicted direction	Questions significant in opposite direction	Questions not significant	Total number of questions
Communication	11 (92%)	0 (0%)	1 (8%)	12
Human interest	3 (20%)	0 (0%)	12 (80%)	15
Other	11 (11%)		91 (89%)	102
Total	25 (19%)		104 (81%)	129

Table **3-4**: Summary of questions significantly associated with foot pointing task.

Conservative Analysis (*n* = 2,690)

Question Topic	Questions significant in predicted direction	Questions significant in opposite direction	Questions not significant	Total number of questions
Communication	8 (67%)	0 (0%)	4 (33%)	12
Human interest	1 (50%)	0 (0%)	1 (50%)	2
Other	4 (25%)		12 (75%)	16
Total	13 (43 %)		17 (57%)	30

Exploratory Analysis (*n* = 1,458 to 10,654)

Question Topic	Questions significant in predicted direction	Questions significant in opposite direction	Questions not significant	Total number of questions
Communication	12 (100%)	0 (0%)	0 (0%)	12
Human interest	2 (13%)	0 (0%)	13 (87%)	15
Other	8 (8%)		94 (92%)	102
Total	22 (17%)		107 (83%)	129

In the gaze sensitivity tasks, the owner placed a treat on the ground and instructed the dog not to eat it. During the first and sixth trials, the owners watched the dog, while the owners had their backs turned for the second and third trials and their eyes covered for the fourth and fifth trials. We analyzed which survey questions predicted the difference in the time it took for dogs to eat the food when they were observed versus when the human's back was turned, as well as when the human's eyes were closed. We identified several questions (five in the pre-survey, six in the full survey) that we predicted would be related to gaze sensitivity. In the conservative analysis, none of these questions were significantly associated with performance in either condition of the task. However, in the exploratory analysis, two questions about gaze sensitivity were significantly associated with dogs waiting longer to eat the food when observed compared to when unobserved, and these relationships were in the expected direction (Table 3-5, Appendix E, Table 3-6, Appendix F). Notably, the two significant questions ("Does {dog name} steal food when you are distracted or not paying attention?" and "Does {dog name} steal food from right under your nose?") were the ones most directly related to the dog stealing prohibited food when unobserved. In contrast, other gaze sensitivity questions, such as those about dogs looking to owners when trying to find a lost toy or frequently seeking and holding eye contact, were not significantly associated with task performance. We also analyzed the average latency to eat prohibited food when the human was not watching to determine if different survey questions were associated with this measure, as it has been suggested to reflect self-control and/or training level (Gnanadesikan et al., 2020). The same two food-stealing questions were again significantly associated with this measure in the expected direction in both analyses (Table 3-7, Appendix G). These questions likely capture both gaze sensitivity and aspects of training. Additionally, other questions related to how well-trained the dog was were significantly associated with latency to eat prohibited food, whereas questions about eye contact and food motivation were not (Table 3-7, Appendix G).

Table **3-5**: Summary of questions significantly associated with gaze sensitivity to back turned task.

Conservative Analysis (*n* = 1,901)				
Question Topic	Questions significant in predicted direction	Questions significant in opposite direction	Questions not significant	Total number of questions
Gaze sensitivity	0 (0%)	0 (0%)	5 (100%)	5
Human interest	0 (0%)	0 (0%)	0 (0%)	0
Other	0 (0%)		25 (100%)	25
Total	0 (0%)		30 (100%)	30
Exploratory Analysis (*n* = 1,230 to 7,593)				
Question Topic	Questions significant in predicted direction	Questions significant in opposite direction	Questions not significant	Total number of questions
Gaze sensitivity	2 (33%)	0 (0%)	4 (67%)	6
Human interest	0 (0%)	0 (0%)	9 (100%)	9
Other	1 (1%)		113 (99%)	114
Total	3 (2%)		126 (98%)	129

Table **3-6**: Summary of questions significantly associated with gaze sensitivity to eyes closed task.

Conservative Analysis (*n* = 1,901)

Question Topic	Questions significant in predicted direction	Questions significant in opposite direction	Questions not significant	Total number of questions
Gaze sensitivity	0 (0%)	0 (0%)	5 (0%)	5
Human interest	0 (0%)	0 (0%)	0 (0%)	0
Other	0 (0%)		25 (100%)	25
Total	0 (0%)		30 (100%)	30

Exploratory Analysis (*n* = 1,230 to 7,592)

Question Topic	Questions significant in predicted direction	Questions significant in opposite direction	Questions not significant	Total number of questions
Gaze sensitivity	2 (33%)	0 (0%)	4 (67%)	6
Human interest	0 (0%)	1 (11%)	8 (89%)	9
Other	3 (3%)		111 (97%)	114
Total	6 (5%)		123 (95%)	129

Table **3-7**: Summary of questions significantly associated with latency to eat prohibited food when unobserved.

Conservative Analysis (*n* = 1,930)

Question Topic	Questions significant in predicted direction	Questions significant in opposite direction	Questions not significant	Total number of questions
Eye contact	0 (0%)	0 (0%)	1 (100%)	1
Food motivation	0 (0%)	0 (0%)	1 (100%)	1
Self-control	0 (0%)	0 (0%)	0 (0%)	0
Training	2 (100%)	0 (0%)	0 (0%)	2
Training/gaze sensitivity	2 (100%)	0 (0%)	0 (0%)	2
Other	8 (33%)		16 (67%)	24
Total	12 (40%)		18 (60%)	30

Exploratory Analysis (*n* = 1,242 to 7,710)

Question Topic	Questions significant in predicted direction	Questions significant in opposite direction	Questions not significant	Total number of questions
Eye contact	0 (0%)	0 (0%)	1 (100%)	1
Food motivation	0 (0%)	1 (20%)	4 (80%)	5
Self-control	1 (100%)	0 (0%)	0 (0%)	1
Training	8 (62%)	0 (0%)	5 (38%)	13
Training/gaze sensitivity	2 (100%)	0 (0%)	0 (0%)	2
Other	22 (21%)		85 (79%)	107
Total	34 (26%)		95 (74%)	129

Three tasks tested dogs' memory by placing food under one of two cups and introducing a delay before allowing the dog to choose. One task measured memory alone, while the other two tested memory against another cognitive ability: communication (by pointing to the incorrect cup) and smell (by switching the food's location while the dog's view was blocked). For the basic memory task, we hypothesized that performance would be associated with survey questions about dogs' memory in everyday life. Seven such questions were identified, all from the pre-survey. Six of these were significantly associated with memory task performance in both the conservative and exploratory analyses, always in the expected direction (i.e., dogs rated as having better memory were more likely to choose the correct cup; Table 3-8, Appendix H). For the memory versus pointing task, we expected memory-related questions to be positively associated with task performance and communication-related questions to be negatively associated, as following the gesture led to the incorrect cup. Three questions addressed both memory and communication (e.g., “Does {dog name} learn new words and gestures with ease?”), meaning their associations could indicate which ability was dominant in the task. Memory-related questions were generally associated with greater reliance on memory in both analyses (Table 3-9, Appendix I). However, communication-related questions were mostly not associated with performance, and in the few significant cases, they were linked to greater reliance on memory rather than gestures—opposite of our predictions. Questions capturing both memory and communication did not predict performance in the conservative analysis, but in the exploratory analysis, two of three were associated with greater memory reliance (Table 3-9, Appendix I). For the memory versus smell task, we expected associations with memory-related questions, as well as those related to smell (since dogs could sniff out the correct location) and hearing (as owners might make audible cues when switching the food). Memory-related questions showed weak associations: none were significant in the conservative analysis, and in the exploratory analysis, results were mixed, with some significant associations in both the expected and opposite directions (Table 3-10, Appendix J). There were few survey questions about smell, but one (“How often does {dog name} sniff other dogs’ urine?”) significantly predicted correct choices in both analyses. Even fewer questions related to hearing, but one (“How often does {dog name} seem to hear things that you don’t?”) was significantly associated with performance in the opposite of the expected direction in the exploratory analysis but was not significant in the conservative analysis (Table 3-10, Appendix J).

Table **3-8**: Summary of questions significantly associated with memory task.

Conservative Analysis (*n* = 1,386)				
Question Topic	Questions significant in predicted direction	Questions significant in opposite direction	Questions not significant	Total number of questions
Memory	6 (86%)	0 (0%)	1 (14%)	7
Other	12 (52%)		11 (48%)	23
Total	18 (60%)		12 (40%)	30
Exploratory Analysis (*n* = 1,011 to 5,607)				
Question Topic	Questions significant in predicted direction	Questions significant in opposite direction	Questions not significant	Total number of questions
Memory	6 (86%)	0 (0%)	1 (14%)	7
Other	20 (16%)		102 (84%)	122
Total	26 (20%)		103 (80%)	129

Table **3-9**: Summary of questions significantly associated with memory versus pointing task.

Conservative Analysis (*n* = 1,573)

Question Topic	Questions significant in predicted direction	Questions significant in opposite direction	Questions not significant	Total number of questions
Memory	3 (75%)	0 (0%)	1 (25%)	4
Memory/communication (direction given with respect to memory)	0 (0%)	0 (0%)	3 (100%)	3
Communication	0 (0%)	1 (11%)	8 (89%)	9
Other	4 (29%)		10 (71%)	14
Total	8 (27%)		22 (73%)	30

Exploratory Analysis (*n* = 1,093 to 6,284)

Question Topic	Questions significant in predicted direction	Questions significant in opposite direction	Questions not significant	Total number of questions
Memory	4 (100%)	0 (0%)	0 (0%)	4
Memory/communication (direction given with respect to memory)	2 (67%)	0 (0%)	1 (33%)	3
Communication	0 (0%)	2 (22%)	7 (78%)	9
Other	31 (27%)		82 (73%)	113
Total	39 (30%)		90 (70%)	0

Table **3-10**: Summary of questions significantly associated with memory versus smell task.

Conservative Analysis (*n* = 1,445)

Question Topic	Questions significant in predicted direction	Questions significant in opposite direction	Questions not significant	Total number of questions
Memory	0 (0%)	0 (0%)	7 (100%)	7
Smell	1 (50%)	0 (0%)	1 (50%)	2
Hearing	0 (0%)	0 (0%)	1 (100%)	1
Other	1 (5%)		19 (95%)	20
Total	2 (7%)		28 (93%)	30

Exploratory Analysis (*n* = 1,039 to 5,822)

Question Topic	Questions significant in predicted direction	Questions significant in opposite direction	Questions not significant	Total number of questions
Memory	3 (43%)	1 (14%)	3 (43%)	7
Smell	1 (25%)	0 (0%)	3 (75%)	4
Hearing	0 (0%)	1 (50%)	1 (50%)	2
Other	8 (7%)		108 (93%)	126
Total	14 (11%)		115 (89%)	129

Two tasks assessed dogs' reasoning abilities: inferential reasoning and physical reasoning. In the inferential reasoning task, a treat was placed under one of two cups without the dog seeing, and one cup was revealed to be empty. Dogs who could infer that the treat must be in the other cup would be able to choose correctly. Five survey questions related to reasoning abilities were identified, all from the pre-survey. None were significantly associated with task performance in the conservative analysis, and in the exploratory analysis, only one ("Does {dog name} ever learn to solve a problem by watching you?") showed a significant association in the expected direction (Table 3-11, Appendix K). Notably, the most directly relevant question ("If {dog name} knows you have food or a toy, but you show {him/her} that one hand is empty, does {he/she} search the other hand?") was not significantly associated with task performance. The physical reasoning task tested similar abilities, so the same survey questions were predicted to be relevant. In this task, a treat was placed in one of two folded pieces of paper, and a successful dog could infer its location based on physical displacement. The same question that was significant in the exploratory analysis of the inferential reasoning task was also significantly associated with physical reasoning performance in both the conservative and exploratory analyses. It was the only reasoning-related question to show a significant association (Table 3-12, Appendix L).

Table **3-11**: Summary of questions significantly associated with inferential reasoning task.

Conservative Analysis (*n* = 1,159)

Question Topic	Questions significant in predicted direction	Questions significant in opposite direction	Questions not significant	Total number of questions
Reasoning	0 (0%)	0 (0%)	5 (100%)	5
Other	2 (8%)		23 (92%)	25
Total	2 (7%)		28 (93%)	30

Exploratory Analysis (*n* = 887 to 4,668)

Question Topic	Questions significant in predicted direction	Questions significant in opposite direction	Questions not significant	Total number of questions
Reasoning	1 (20%)	0 (0%)	4 (80%)	5
Other	7 (6%)		117 (94%)	124
Total	8 (6%)		121 (94%)	129

Table **3-12**: Summary of questions significantly associated with physical reasoning task.

Conservative Analysis (*n* = 1,132)

Question Topic	Questions significant in predicted direction	Questions significant in opposite direction	Questions not significant	Total number of questions
Reasoning	1 (20%)	0 (0%)	4 (80%)	5
Other	4 (16%)		21 (84%)	25
Total	5 (17%)		25 (83%)	30

Exploratory Analysis (*n* = 865 to 4,512)

Question Topic	Questions significant in predicted direction	Questions significant in opposite direction	Questions not significant	Total number of questions
Reasoning	1 (20%)	0 (0%)	4 (80%)	5
Other	10 (8%)		114 (92%)	124
Total	11 (9%)		118 (91%)	129

Discussion

Dog cognition tasks have previously been used to inform theoretical understandings of how domestication has changed the way dogs think (Hansen Wheat et al., 2023; Miklósi et al., 2003b; Salomons et al., 2021) and are being applied to select dogs for performing specific jobs (Hare & Ferrans, 2021; MacLean & Hare, 2018). However, to be able to interpret the results of these tasks correctly, we need to know whether performance on these tasks correlates with external observations of dogs' behavior in the real world. We addressed this need by examining whether dog cognition task performance in an extensive citizen science dataset is associated with owner ratings of their dogs in a survey.

Overall, these results provide strong evidence that tasks assessing communication, memory, and eating prohibited food are valid measures of real-world behavior. The task contrasting memory with gesture comprehension primarily reflects dogs' memory. The memory versus smell task seems to assess memory but offers only weak validation as a measure of a dog's real-world reliance on scent. Tests of inferential and physical reasoning bear some weak associations with owner-reported reasoning abilities. The eye contact task may partially measure empathy but is confounded by food motivation, making the Dognition version of this task unreliable as a valid measure of empathy. Future studies should investigate whether eye contact maintained in the absence of a treat is a more valid measure of a dog's empathy.

This work makes a significant contribution to the limited body of research validating dog cognition tasks against real-world behavior measured with surveys and observations. To our knowledge, this study represents the largest sample size of any attempt to validate dog cognition tasks. Several tasks are validated here that, as of now, have not been investigated for their correlation with real-world behavior in dogs. The large sample size of this study provides a capacity for high statistical power, offering future researchers a valuable frame for understanding the likely magnitude of effect sizes when correlating cognitive tasks with survey-based behavioral measurements.

The Dognition citizen science dataset analyzed in this study has been utilized in several other published studies, and the validation of these cognitive tasks helps to contextualize previous findings derived from this dataset. For example, the first published assessment of Dognition data included a factor analysis, identifying factors that the authors interpreted as measuring cooperative communication, reasoning about others' visual perceptions, memory processes, reasoning, and eye contact (Stewart et al., 2015). Our findings support their interpretations regarding communication, memory, and reasoning as latent variables measured by these tasks. However, what Stewart et al. interpreted as reasoning about other's visual perceptions may, in fact, be more accurately described as a tendency to steal food when humans are not looking, which requires gaze sensitivity but is not synonymous with it. The eye contact dimension, left uninterpreted by Stewart et al. but described to Dognition participants as a measure of empathy, is challenging to interpret due to the confounding factor of food motivation. While Stewart et al.

suggested that their results refuted the existence of a general factor of intelligence in dogs, our analyses urge caution in this interpretation. Our results show that various survey questions correlated with memory, communication, and reasoning tasks were also correlated with the other tasks, and the gaze sensitivity and eye contact tasks may represent aspects of the dog's preferences and interests rather than purely cognitive information processing abilities.

Other Dognition studies have explored the relationship between dogs' cognitive performance and demographic factors such as sex, age, and breed, and this study provides insights that help interpret these findings. For instance, Watowich et al., using the Dognition dataset, noted that male dogs made significantly more eye contact than female dogs (Watowich et al., 2020), whereas a study of dogs given exogenous oxytocin found that female dogs made more eye contact with their owners (Nagasawa et al., 2015). While the administration of oxytocin could account for this contradiction, our study highlights the differences in interest in the treat could be a confounding factor. Regarding age, an analysis of the Dognition dataset found that memory tasks in particular were best modelled as a negative quadratic function of age, with memory ability increasing early in life and then declining with age (Watowich et al., 2020). Our findings also show that the memory task was associated with various memory-related abilities in dogs, including remembering where lost toys are located and remembering words. Future research could investigate whether age-related declines occur with all memory-related tasks or if certain forms of memory, such as crystallized memory, remain preserved, while others, like fluid memory, decline, as has been observed in humans (Tucker-Drob et al., 2022). With respect to breed differences, Horschler et al. found that dog breeds with larger brains performed better on memory tasks and waited longer to get food in the cunning task (Horschler et al., 2019). In light of our findings, this indicates a link between brain size and both memory and trainability. Additionally, Gnanadesikan et al. found that the gesture following task and the time waited to get prohibited food were the most genetically heritable tasks when using breed-averaged data

(Gnanadesikan et al., 2020), and in light of this study, communicative ability and trainability are likely the traits being measured.

In addition to contextualizing findings that rely on the Dognition dataset, this study also helps contextualize findings relying on similar tasks to interpret how cognition is related to domestication and working roles. For example, it has been found that dogs follow human pointing gestures at a higher rate than wolves, which has been used to argue that dogs evolved the ability to communicate with humans in a cooperative context (Hare et al., 2002; Salomons et al., 2021, 2023). Similar findings in experimentally domesticated foxes have been used to strengthen the argument that these communicative abilities are the result of domestication (Hare et al., 2005). However, others have argued that these differences are overstated and that the main difference between dogs and wolves is their interest in humans, which could be driving the results (Hansen Wheat et al., 2023). This study validates that the pointing task seems to be measuring the communicative ability of dogs, extending even beyond gestural communication specifically, which suggest that performance on this task is not merely explained by interest in humans. This provides evidence in support of the interpretation that dogs outperforming wolves on a pointing task indicates higher levels of communicative ability towards humans. MacLean et al. found that cognitive tasks, including some that were substantially similar methodologically to those in Dognition, were predictive of success in working dogs (MacLean & Hare, 2018). The success of military working dogs was associated especially strongly with performance on memory and gesture-following tasks (MacLean & Hare, 2018).

The findings of this current paper indicate that these tasks are measuring real-world instances of good memory and communication in dogs that affect the way they interact with humans and their environments. This includes traits like the ability to understand more words, which it is easy to imagine being useful for working dogs. In light of that, it is not surprising that a dog job like detection, which involves learning to understand the directions of a human handler, would hinge on abilities measured by these tasks. Nagasawa et al. found a link between administered oxytocin in dogs and prolonged eye contact with humans, which was used to interpret eye contact as a measure of social bonding between these two species (Nagasawa et al., 2015). While the results from Dognition are confounded by the presence of a treat by the eye, the correlation with some measures of empathy indicates that this may nevertheless have some validity.

In addition to contributing to our understanding of dogs, this work also contributes to our understanding of human cognition. Dogs can be a useful model for understanding human evolution and especially human communication and cooperation (Chapter 2). Dogs are more successful at following human gestures than even our closest living relatives: the chimpanzees (Hare et al., 2002). It has been argued that this is the result of convergent evolutionary pressures in humans and dogs leading humans to undergo a type of self-domestication (Hare, 2017; Wrangham, 2019). As the structure of individual differences in cognitive tasks in human infants is more like that of dogs than to chimpanzees (MacLean et al., 2017), there appears to be some about of cognitive convergence of dogs with humans. In this study, we found that dogs' comprehension of human gestures is associated with various other communicative abilities, including the number of words understood. As gesture comprehension has been a key component of arguments that dogs' social cognition has converged with humans (Hare & Tomasello, 2005; MacLean et al., 2017), the current study helps contextualize this and event points to its relevance to understanding topics like human language. In addition, dogs are an especially useful model for understanding the factors affecting human health (Chapter 2), and this extends to the cognitive domain as well. Like humans, dogs can experience a decline in certain cognitive abilities, such as memory, as they age (Watowich et al., 2020). As dogs live in the same environments as humans and are exposed to many of the same environmental conditions, they are a promising model for human aging and may help us identify critical environmental variables or potential treatments for a variety of age-related conditions (Hoffman et al., 2018; Ruple et al., 2022). This may also be true when it comes to dementia. For instance, canine cognitive disfunction syndrome in aging dogs is associated with periodontal disease and particularly with *Porphyromonas gingivalis* and *Leptotrichia*, and in humans, these are also associated with Alzheimer's disease (Templeton et al., 2023). Research like the present study that discovers the behavioral associations of cognitive tests in dogs will improve our ability to use dogs as a model for cognitive aging in humans.

Several benefits of this validation study are apparent for future work. As dog cognition tasks have been found to be effective for predicting the success of working dogs (MacLean & Hare, 2018), the finding that cognitive tasks and owner ratings are correlated supports the possibility of using either of these methods to select working dogs. Cognition tasks have the advantage of being usable on a population of dogs that is not well known, unlike owner surveys. However, cognitive tasks are time consuming to perform on a large population of dogs, so surveying people who know their dogs well can be a more time efficient way to compare dogs. Both cognition tasks and surveys have strengths and weaknesses for selecting working dogs, so there may be reasons to employ both in different contexts or in concert. The validation of the cognitive tasks in this study is useful for improving interpretations of other studies that use similar tasks. Whether the tasks are used to compare dogs and wolves to learn about domestication, to compare different populations of dogs to see how they differ, or to evaluate the effects of interventions on dog cognition, validation of these tasks improves researchers’ ability to interpret the results. Finally, anthropologists looking to compare dog populations around the world may benefit from being able to perform these cognitive tasks, as the linguistic and cultural challenges of translating surveys may make them less comparable across cultures than cognitive tasks with dogs.

References

Ameen, C., Feuerborn, T. R., Brown, S. K., Linderholm, A., Hulme-Beaman, A., Lebrasseur, O., Sinding, M. H. S., Lounsberry, Z. T., Lin, A. T., Appelt, M., Bachmann, L., Betts, M., Britton, K., Darwent, J., Dietz, R., Fredholm, M., Gopalakrishnan, S., Goriunova, O. I., Grønnow, B., … Evin, A. (2019). Specialized sledge dogs accompanied Inuit dispersal across the North American Arctic. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1916). https://doi.org/10.1098/rspb.2019.1929

Balme, J., O'Connor, S., & Fallon, S. (2018). New dates on dingo bones from Madura Cave provide oldest firm evidence for arrival of the species in Australia. *Scientific Reports*, *8*(1), 4–9. https://doi.org/10.1038/s41598-018-28324-x

Bergström, A., Frantz, L., Schmidt, R., Ersmark, E., Lebrasseur, O., Girdland-Flink, L., Lin, A. T., Storå, J., Sjögren, K.-G., Anthony, D., Antipina, E., Amiri, S., Bar-Oz, G., Bazaliiskii, V. I., Bulatović, J., Brown, D., Carmagnini, A., Davy, T., Fedorov, S., … Skoglund, P. (2020). Origins and genetic legacy of prehistoric dogs. *Science*, *370*(557–564), 1–7.

Brady, K., Hewison, L., Wright, H., Zulch, H., Cracknell, N., & Mills, D. (2018). A spatial discounting test to assess impulsivity in dogs. *Applied Animal Behaviour Science*, *202*(July 2017), 77–84. https://doi.org/10.1016/j.applanim.2018.01.003

Chambers, J., Quinlan, M. B., Evans, A., & Quinlan, R. J. (2020). Dog-human coevolution: cross-cultural analysis of multiple hypotheses. *Journal of Ethnobiology*, *40*(4), 414–433. https://doi.org/10.2993/0278-0771-40.4.414

Cipriani, L. (1966). *The Andaman Islanders* (D. T. Cox & L. Cole, Eds.). Frederick A. Praeger, Inc. https://ehrafworldcultures-yale-edu.ezaccess.libraries.psu.edu/document?id=az02-011.%0A

Coppinger, L., & Coppinger, R. (2000). Dogs for herding and guarding livestock. In T. Grandin (Ed.), *Livestock Handling and Transport* (2nd ed., pp. 235–253).

Fillios, M. A., & Taçon, P. S. C. (2016). Who let the dogs in? A review of the recent genetic evidence for the introduction of the dingo to Australia and implications for the movement of people. *Journal of Archaeological Science: Reports*, *7*, 782–792. https://doi.org/10.1016/j.jasrep.2016.03.001

Freedman, A. H., & Wayne, R. K. (2017). Deciphering the origin of dogs: from fossils to genomes. *Annual Review of Animal Biosciences*, *5*(1), 281–307. https://doi.org/10.1146/annurev-animal-022114-110937

Gnanadesikan, G. E., Hare, B., Snyder-Mackler, N., & MacLean, E. L. (2020). Estimating the heritability of cognitive traits across dog breeds reveals highly heritable inhibitory control and communication factors. *Animal Cognition*, *23*(5), 953–964. https://doi.org/10.1007/s10071-020-01400-4

Greig, K., Boocock, J., Allen, M. S., Matisoo-Smith, L., & Walter, R. (2018). Ancient DNA evidence for the introduction and dispersal of dogs (Canis familiaris) in New Zealand. *Journal of Pacific Archaeology*, *9*(1), 1–10.

Guagnin, M., Perri, A. R., & Petraglia, M. D. (2018). Pre-Neolithic evidence for dog-assisted hunting strategies in Arabia. *Journal of Anthropological Archaeology*, *49*(November 2017), 225–236. https://doi.org/10.1016/j.jaa.2017.10.003

Hall, N. J., Johnston, A. M., Bray, E. E., Otto, C. M., MacLean, E. L., & Udell, M. A. R. (2021). Working dog training for the twenty-first century. *Frontiers in Veterinary Science*, *8*(July), 1–18. https://doi.org/10.3389/fvets.2021.646022

Hansen Wheat, C., van der Bijl, W., & Wynne, C. D. L. (2023). Rearing condition and willingness to approach a stranger explain differences in point following performance in wolves and dogs. *Learning and Behavior*, *51*(2), 127–130. https://doi.org/10.3758/s13420-022-00544-2

Hare, B. (2017). Survival of the friendliest: Homo sapiens evolved via selection for prosociality. *Annual Review of Psychology*, *68*(1), 155–186. https://doi.org/10.1146/annurev-psych-010416-044201

Hare, B., Brown, M., Williamson, C., & Tomasello, M. (2002). The domestication of social cognition in dogs. *Science*, *298*(5598), 1634–1636. https://doi.org/10.1126/science.1072702

Hare, B., & Ferrans, M. (2021). Is cognition the secret to working dog success? *Animal Cognition*, *24*(2), 231–237. https://doi.org/10.1007/s10071-021-01491-7

Hare, B., Plyusnina, I., Ignacio, N., Schepina, O., Stepika, A., Wrangham, R., & Trut, L. (2005). Social cognitive evolution in captive foxes is a correlated by-product of experimental domestication. *Current Biology*, *15*, 226–230. https://doi.org/10.1016/j

Hare, B., & Tomasello, M. (2005). Human-like social skills in dogs? *Trends in Cognitive Sciences*, *9*(9), 439–444. https://doi.org/10.1016/j.tics.2005.07.003

Hoffman, J. M., Creevy, K. E., Franks, A., O'Neill, D. G., & Promislow, D. E. L. (2018). The companion dog as a model for human aging and mortality. *Aging Cell*, *17*(3). https://doi.org/10.1111/acel.12737

Hole, F., & Wyllie, C. (2007). The oldest depictions of canines and a possible early breed of dog in Iran. *Paléorient*, *33*(1), 175–185. https://doi.org/10.3406/paleo.2007.5213

Horschler, D. J., Hare, B., Call, J., Kaminski, J., Miklósi, Á., & MacLean, E. L. (2019). Absolute brain size predicts dog breed differences in executive function. *Animal Cognition*, *22*(2), 187–198. https://doi.org/10.1007/s10071-018-01234-1

Hsu, Y., & Serpell, J. A. (2003). Development and validation of a questionnaire for measuring behavior and temperament traits in pet dogs. *Journal of the American Veterinary Medical Association*, *223*(9).

Jones, R. (1970). Tasmanian Aborigines and dogs. *Mankind*, *7*(4), 256–271. https://doi.org/10.1111/j.1835-9310.1970.tb00420.x

Lupo, K. D. (2017). When and where do dogs improve hunting productivity? The empirical record and some implications for early Upper Paleolithic prey acquisition. *Journal of Anthropological Archaeology*, *47*, 139–151. https://doi.org/10.1016/j.jaa.2017.05.003

Lupo, K. D. (2019). Hounds follow those who feed them: What can the ethnographic record of hunter-gatherers reveal about early human-canid partnerships? *Journal of Anthropological Archaeology*, *55*(April), 101081. https://doi.org/10.1016/j.jaa.2019.101081

MacLean, E. L., & Hare, B. (2018). Enhanced selection of assistance and explosive detection dogs using cognitive measures. *Frontiers in Veterinary Science*, *5*(236), 1–14. https://doi.org/10.3389/fvets.2018.00236

MacLean, E. L., Herrmann, E., Suchindran, S., & Hare, B. (2017). Individual differences in cooperative communicative skills are more similar between dogs and humans than chimpanzees. *Animal Behaviour*, *126*, 41–51. https://doi.org/10.1016/j.anbehav.2017.01.005

Martin, P., & Bateson, P. (2017). *Measuring behaviour: an introductory guide* (3rd ed.). Cambridge University Press.

McPeake, K. J., Collins, L. M., Zulch, H., & Mills, D. S. (2021). Behavioural and physiological correlates of the Canine Frustration Questionnaire. *Animals*, *11*(3346), 1–15.

Miklósi, Á. (2015). *Dog behaviour, evolution, and cognition* (2nd ed.). Oxford University Press.

Miklósi, Á., Kubinyi, E., Topál, J., Gácsi, M., Virányi, Z., & Csányi, V. (2003a). A simple reason for a big difference: Wolves do not look back at humans, but dogs do. *Current Biology*, *13*(13), 763–766. https://doi.org/10.1016/S

Miklósi, Á., Kubinyi, E., Topál, J., Gácsi, M., Virányi, Z., & Csányi, V. (2003b). A simple reason for a big difference: Wolves do not look back at humans, but dogs do. *Current Biology*, *13*(13), 763–766. https://doi.org/10.1016/S

Mongillo, P., Scandurra, A., Eatherington, C. J., D'Aniello, B., & Marinelli, L. (2019). Development of a spatial discount task to measure impulsive choices in dogs. *Animals*, *9*(7), 1–14. https://doi.org/10.3390/ani9070469

Nagasawa, M., Mitsui, S., En, S., Ohtani, N., Ohta, M., Sakuma, Y., Onaka, T., Mogi, K., & Kikusui, T. (2015). Oxytocin-gaze positive loop and the coevolution of human-dog bonds. *Science*, *348*(6232), 333–336.

Perri, A. R. (2020). Prehistoric dogs as hunting weapons: the advent of animal biotechnology. In B. Berthke & A. Burtt (Eds.), *Dogs: Archaeology of the Human-Canine Connection Beyond Domestication* (pp. 7–44). University Press of Florida.

Perri, A. R., Feuerborn, T. R., Frantz, L. A. F., Larson, G., & Malhi, R. S. (2021). Dog domestication and the dual dispersal of people and dogs into the Americas. *Proceedings of the National Academy of Sciences*, *118*(6), 1–8. https://doi.org/10.1073/pnas.2010083118

Pitulko, V. V., & Kasparov, A. K. (2017). Archaeological dogs from the Early Holocene Zhokhov site in the Eastern Siberian Arctic. *Journal of Archaeological Science: Reports*, *13*(May), 491–515. https://doi.org/10.1016/j.jasrep.2017.04.003

Ruple, A., Maclean, E., Snyder-Mackler, N., Creevy, K. E., & Promislow, D. (2022). Dog models of aging. *Annual Review of Animal Biosciences*, *10*, 419–439. https://doi.org/10.1146/annurev-animal-051021-080937

Saavedra-Aracena, L., Grimm-Seyfarth, A., & Schüttler, E. (2021). Do dog-human bonds influence movements of free-ranging dogs in wilderness? *Applied Animal Behaviour Science*, *241*(April), 105358. https://doi.org/10.1016/j.applanim.2021.105358

Salomons, H., Smith, K. C. M., Callahan-Beckel, M., Callahan, M., Levy, K., Kennedy, B. S., Bray, E. E., Gnanadesikan, G. E., Horschler, D. J., Gruen, M., Tan, J., White, P., VonHoldt, B. M., MacLean, E. L., & Hare, B. (2021). Cooperative communication with humans evolved to emerge early in domestic dogs. *Current Biology*, *31*(July), 1–8. https://doi.org/10.1016/j.cub.2021.06.051

Salomons, H., Smith, K. C. M., Callahan-Beckel, M., Callahan, M., Levy, K., Kennedy, B. S., Bray, E. E., Gnanadesikan, G. E., Horschler, D. J., Gruen, M., Tan, J., White, P., VonHoldt, B. M., MacLean, E. L., & Hare, B. (2023). Response to Hansen Wheat et al.: additional analysis further supports the early emergence of cooperative communication in dogs compared to wolves raised with more human exposure. *Learning and Behavior*, *51*(2), 131–134. https://doi.org/10.3758/s13420-023-00576-2

Serpell, J. A. (2021). Commensalism or cross-species adoption? A critical review of theories of wolf domestication. *Frontiers in Veterinary Science*, *8*(April), 1–10. https://doi.org/10.3389/fvets.2021.662370

Shannon, L. M., Boyko, R. H., Castelhano, M., Corey, E., Hayward, J. J., McLean, C., White, M. E., Said, M. A., Anita, B. A., Bondjengo, N. I., Calero, J., Galov, A., Hedimbi, M., Imam, B., Khalap, R., Lally, D., Masta, A., Oliveira, K. C., Pérez, L., … Boyko, A. R. (2015). Genetic structure in village dogs reveals a Central Asian domestication origin. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(44), 13639–13644. https://doi.org/10.1073/pnas.1516215112

Shettleworth, S. J. (2010). *Cognition, evolution, and behavior* (2nd ed.). Oxford University Press.

Stevens, J. R., Mathias, M., Herridge, M., Hughes-Duvall, K., Wolff, L. M., & Yohe, M. (2022). Do owners know how impulsive their dogs are? *Animal Behavior and Cognition*, *9*(3), 261–286.

Stewart, L., MacLean, E. L., Ivy, D., Woods, V., Cohen, E., Rodriguez, K., McIntyre, M., Mukherjee, S., Call, J., Kaminski, J., Miklósi, Á., Wrangham, R. W., & Hare, B. (2015). Citizen science as a new tool in dog cognition research. *PLoS ONE*, *10*(9), 1–16. https://doi.org/10.1371/journal.pone.0135176

Svartberg, K. (2005). A comparison of behaviour in test and in everyday life: Evidence of three consistent boldness-related personality traits in dogs. *Applied Animal Behaviour Science*, *91*(1–2), 103–128. https://doi.org/10.1016/j.applanim.2004.08.030

Templeton, G. B., Fefer, G., Case, B. C., Roach, J., Azcarate-Peril, M. A., Gruen, M. E., Callahan, B. J., & Olby, N. J. (2023). Longitudinal analysis of canine oral microbiome using whole genome sequencing in aging companion dogs. *Animals*, *13*(24). https://doi.org/10.3390/ani13243846

Thalmann, O., Shapiro, B., Cui, P., Schuenemann, V. J., Sawyer, S. K., Greenfield, D. L., Germonpré, M. B., Sablin, M. V., López-Giráldez, F., Domingo-Roura, X., Napierala, H., Uerpmann, H.-P., Loponte, D. M., Acosta, A. A., Giemsch, L., Schmitz, R. W., Worthington, B., Buikstra, J. E., Druzhkova, A., … Wayne, R. K. (2013). Complete mitochondrial genomes of ancient canids suggest a European origin of domestic dogs. *Science*, *342*(November), 871–874.

Tucker-Drob, E. M., de la Fuente, J., Köhncke, Y., Brandmaier, A. M., Nyberg, L., & Lindenberger, U. (2022). A strong dependency between changes in fluid and crystallized abilities in human cognitive aging. *Science Advances*, *8*(5), 1–10. https://doi.org/10.1126/sciadv.abj2422

Vilà, C., Savolainen, P., Maldonado, J. E., Amorim, I. R., Rice, J. E., Honeycutt, R. L., Crandall, K. A., Lundeberg, J., & Wayne, R. K. (1997). Multiple and ancient origins of the domestic dog. *Science*, *276*(5319), 1687–1689.

Wang, G. D., Zhai, W., Yang, H. C., Wang, L., Zhong, L., Liu, Y. H., Fan, R. X., Yin, T. T., Zhu, C. L., Poyarkov, A. D., Irwin, D. M., Hytönen, M. K., Lohi, H., Wu, C. I., Savolainen, P., & Zhang, Y. P. (2016). Out of southern East Asia: The natural history of domestic dogs across the world. *Cell Research*, *26*(1), 21–33. https://doi.org/10.1038/cr.2015.147

Watowich, M. M., MacLean, E. L., Hare, B., Call, J., Kaminski, J., Miklósi, Á., & Snyder-Mackler, N. (2020). Age influences domestic dog cognitive performance independent of average breed lifespan. *Animal Cognition*, *0123456789*. https://doi.org/10.1007/s10071-020-01385-0

Wrangham, R. W. (2019). Hypotheses for the evolution of reduced reactive aggression in the context of human self-domestication. *Frontiers in Psychology*, *10*(August), 1–11. https://doi.org/10.3389/fpsyg.2019.01914

Chapter 4

A Comparison of Dog Cognitive Tasks, Owner Perceptions, and Observations in a Dog Park

Introduction

Cognition refers to the set of processes an organism uses to gather information from its environment, process that information, and respond accordingly (Shettleworth, 2010). Comparative studies of animal performance on shared cognitive tasks have revealed interspecies differences, which are often interpreted as outcomes of evolutionary pressures that shape species to meet the demands of their distinct environments (MacLean et al., 2014; Rosati, 2017). Our understanding of the evolution of cognition can be enriched by integrating the four questions identified by Niko Tinbergen as the aims of ethology (MacLean et al., 2012; Shettleworth, 2001). These are: the triggering causal process, the ontogenetic development over an individual's lifetime, the phylogenetic history of its evolution, and the function it serves in terms of evolutionary fitness (Tinbergen, 1963). The last of these, the function, is crucial for linking cognition to the third question, evolutionary change over time. For cognition to be subject to natural selection, it must exhibit individual variation that is at least partially heritable and must influence fitness—specifically, survival and reproduction. Thus, understanding how internal cognitive processes translate into external behavior is essential for studying the evolution of cognition.

Dogs are an especially useful model with which to study the evolution of cognition and its relationship to behavior. Domesticated from gray wolves in the Late Pleistocene in Eurasia (Freedman & Wayne, 2017; Shannon et al., 2015; Thalmann et al., 2013; Wang et al., 2016), dogs were remarkably successful at spreading alongside human societies across Eurasia and into Africa, Australia, the Americas, Polynesia, and the Arctic (Ameen et al., 2019; Balme et al., 2018; Bergström et al., 2020; Greig et al., 2018; Perri et al., 2021). Across this wide range of environments, ranging from the tropics to the Arctic and from foraging to pastoralist and agriculturalist societies, dogs have served a diverse array of functions. For thousands of years, they have assisted humans in detecting, tracking, and capturing prey (Guagnin et al., 2018; Koungoulos & Fillios, 2020; Perri, 2020). In pastoralist and agriculturalist societies, dogs have guarded and herded livestock (Coppinger & Coppinger, 2000). In some regions, dogs have also supported human mobility by pulling sleds or travois (Lupo, 2019; Pitulko & Kasparov, 2017; Welker & Byers, 2019). There are also more novel roles that dogs have taken on in recent history, such as assisting people with disabilities and detecting contraband (Hall et al., 2021). Beyond their functional roles, dogs also serve as companions, and, in many societies, are considered family members (Chambers et al., 2020; Pew Research Center, 2006).

Dogs' remarkable success in spreading across the globe, cooperating with humans, and forming close social bonds may in part be attributed to their cognitive abilities. Comparative studies show that dogs outperform wolves in understanding human gestures, such as pointing and novel cues—a difference that is evident even in young puppies compared to highly socialized wolves (Hare et al., 2002; Salomons et al., 2021). Similar findings have emerged from research on domesticated foxes, where those selectively bred for tameness across generations show enhanced responsiveness to human gestures compared to control foxes bred without selection (Hare et al., 2005). When confronted with an unsolvable task, such as accessing food in a sealed container, dogs are more likely than wolves to look to humans for help, suggesting an evolved tendency to seek cooperative interaction (Miklósi et al., 2003; Salomons et al., 2021). However, this advantage appears specific to social cognition. On nonsocial tasks, such as those testing memory or self-control, dogs and wolves perform similarly (Salomons et al., 2021).

Taken together, these findings indicate that domestication has resulted in cognitive changes in dogs specifically in the social domain (Hare et al., 2005; Salomons et al., 2021). However, the exact mechanisms by which selection acted on these social cognitive traits during domestication remain unclear. In the domesticated fox experiment, for instance, animals were not selected for gesture comprehension or other cognitive traits, but for a lack of fear and aggression towards humans, and then once this had been lost, they were selected for the behavior of eagerly seeking out contact with humans (Trut et al., 2009). This suggests that enhanced social cognition may have arisen as a pleiotropic by-product of selection on other behavioral traits (Hare et al., 2005; A. S. Wilkins et al., 2014). Nonetheless, in early domesticated contexts, where food scarcity was common, behaviors that elicited provisioning from humans likely conferred significant fitness advantages. Indeed, in many parts of the world, dogs that excelled at tasks such as hunting and hauling were often rewarded with extra food (Lupo, 2019). This raises the possibility that the success of dogs at particular jobs may have increased their fitness. Supporting this, cognition has been identified as a crucial factor that can determine the success of working dogs (Hare & Ferrans, 2021; MacLean & Hare, 2018). When military detection dogs were given a battery of cognitive tasks, various tasks (including gesture comprehension and working memory) were found to significantly predict the success of these dogs (MacLean & Hare, 2018). Similarly, cognitive test batteries have been shown to predict which dogs are most likely to succeed as assistance animals for people with disabilities (MacLean & Hare, 2018). While these studies do not yet pinpoint how individual cognitive differences translate into real-world working behaviors, they suggest that dogs' cognitive abilities play a critical role in shaping their interactions with humans and their environments.

Relatively few studies have investigated the degree to which cognitive measures obtained in a laboratory setting reflect dogs' behavior in naturalistic contexts. Real-world dog behavior can be assessed in several ways, including direct observation using ethograms— a structured list of defined behaviors—or indirectly through owner-completed surveys that capture perceived behavioral tendencies (Miklósi, 2015). In one large study, hundreds of dogs were assessed through both cognitive tasks and owner surveys. Both approaches consistently captured traits such as sociability, fearlessness, and playfulness, although measures of aggression showed less agreement between methods (Svartberg, 2005). Laboratory tests designed to measure frustration of dogs correlated with owner ratings of the dogs' frustration (McPeake et al., 2021). Free-ranging dogs who exhibited more exploratory behavior in lab tests were also found to travel longer distances when monitored via GPS collars (Saavedra-Aracena et al., 2021). However, efforts to validate lab-based measures of impulsivity have produced mixed results, with some studies finding correlations and others not (Brady et al., 2018; Mongillo et al., 2019; Stevens et al., 2022).

To better understand the relationship between dog cognition and real-world behavior, we administered a battery of cognitive tasks to pet dogs and collected multiple measures of their behavior outside the laboratory. Specifically, we conducted 30-minute focal follows in an off-leash dog park, where dogs could move freely and engage in spontaneous interactions with other dogs and humans. This setting allowed us to observe their natural behavior in a relatively unconstrained environment. In addition, we asked owners to complete surveys about their dogs prior to witnessing their performance in the cognitive tasks. These surveys included the Canine Behavioral Assessment and Research Questionnaire (C-BARQ), a widely used instrument for assessing behaviors related to aggression and fear (V. Wilkins et al., 2024), and the Monash Canine Personality Questionnaire–Revised (MCPQ-R), which measures broader personality traits (Ley et al., 2008). This helps contextualize the interpretations of these cognitive tasks and gives guidance to future studies planning on incorporating them into the study of dogs.

Methods

Data collection

To compare laboratory measurements of dogs' cognition and temperaments to owner assessments and behavioral observations, we recruited 56 pet dogs from Tudek Dog Park in State College, Pennsylvania, USA. Dog owners attending the dog park with their dogs were approached about participating in the study, and if they consented, they participated either at that moment or at another scheduled time. The sample population included purebred and mixed-breed dogs with ages ranging from under 4 months to 9 years old (median age: 2 years). The sex distribution was 46% females and 54% males, with 79% of individuals reported as spayed or neutered.

The dogs' guardians filled out surveys to provide basic demographic information as well as insights into their dogs' personality traits and behavioral tendencies. Specifically, they filled out two previously validated instruments: the Monash Canine Personality Questionnaire-Revised (MCPQ-R) (Ley et al., 2008) and the shortened Canine Behavioral Assessment and Research Questionnaire (C-BARQ$^{(S)}$) (V. Wilkins et al., 2024).

Dogs were observed for a 30-minute focal follow in Tudek Dog Park, with the session video recorded for later analysis. Guardians were instructed to behave as they normally would during a visit to the dog park. The researcher kept track of the number of people and dogs present in the park (both from the household and others) so that its effect on behavior could be controlled. Using BORIS (Friard & Gamba, 2016), the videos were later coded for the time the focal dog spent within 1 meter of other dogs and humans, as well as for play-initiation behaviors, stress behaviors, and aggressive behaviors, following published ethograms (Ottenheimer Carrier et al., 2013).

On a separate day from the dog park observation, dogs participated in a series of cognitive and temperament tasks (Figure 4-1). During these sessions, the dog's guardian held the dog in the center of the room while a researcher set up and administered each task. All tasks were designed to assess internal cognitive processes and temperament traits, with food rewards used as motivation.

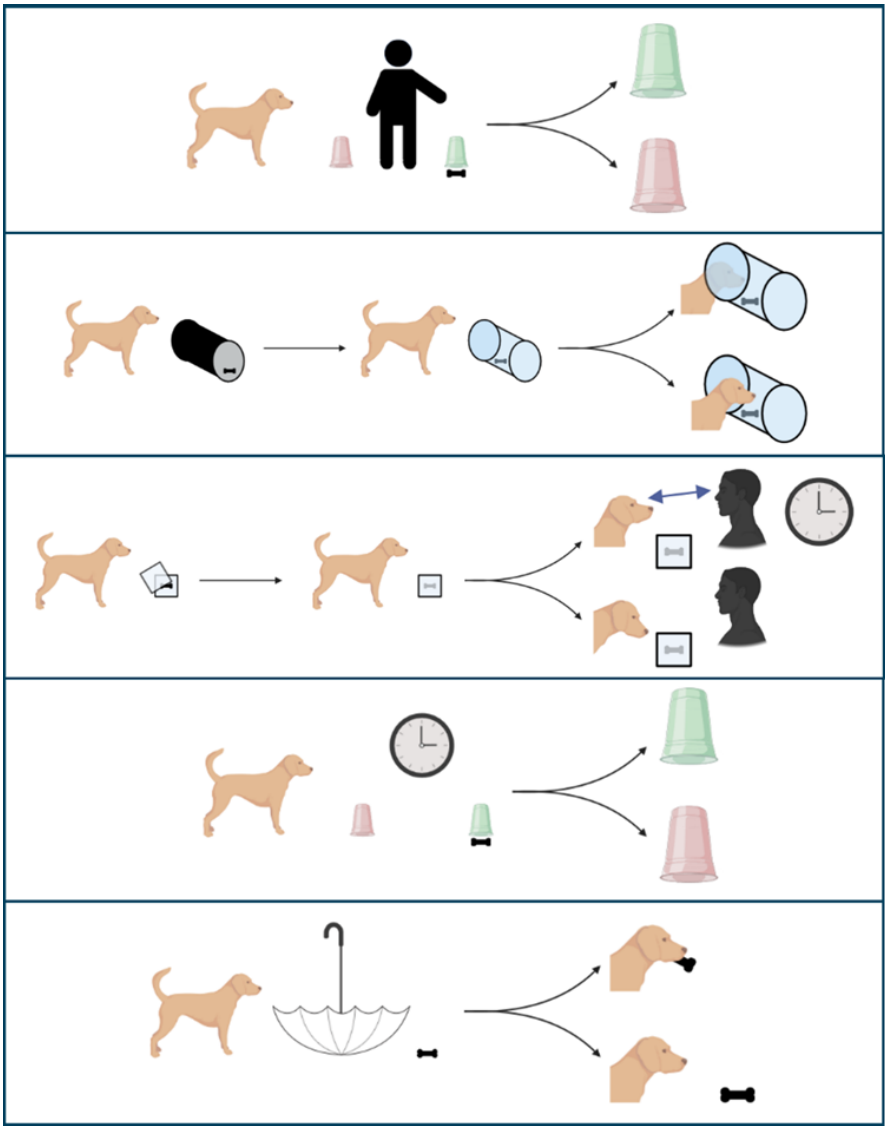

Figure **4-1**: Graphical representation of the cognitive tasks performed in this study. From top to bottom: the pointing task, the inhibitory control cylinder task, the impossible task, the memory task, and the umbrella temperament task. Single straight-line arrow indicates progression to the actual task from the familiarization period. Divergent curved arrows represent the possible outcomes of each trial.

The first task was a pointing task, which has previously been used to assess dogs' sensitivity to human communication cues (Hare et al., 2002). Food was placed under one of two cups, with the dog blocked from seeing which cup. The researcher then pointed with an extended arm towards the cup with the treat, and the guardian released the dog to choose either cup by touching it or putting its face over it. After ten trials of pointing with an extended arm, another ten trials were conducted with the arm across the body. Finally, ten trials were conducted in which the dog saw where the treat was placed, but the researcher then pointed to the incorrect cup, assessing whether dogs relied on human cues or their own observations. Note that the latter two versions of the task were added midway through the study to increase the ability to distinguish between dogs on this task.

The second task was one designed to measure inhibitory control (MacLean et al., 2014). After four familiarization trials using an opaque cylinder, dogs were presented with a transparent cylinder. Across ten test trials, researchers recorded whether the dog touched the transparent barrier before successfully retrieving the treat, indicating impulse control.

The third task, often referred to as the unsolvable task or impossible task, has been controversially claimed to measure dogs' production of communication (Miklósi et al., 2003). Dogs were shown a treat that was placed into a plastic box. To familiarize the dog, the dog was able to retrieve the treat four times by knocking the loosely placed lid off the box. Then, four test trials were conducted in which the lid to the box was sealed. Over each 30 second trial, the amount of eye contact with the experimenter was measured using a stopwatch.

The fourth task involved short-term memory (Stewart et al., 2015). The dog watched as the researcher placed a treat under one of two cups. The dog was restrained for varying lengths of time for each of the four trials (30, 60, 90, and 120 seconds) before choosing either cup in the manner described in the pointing task above.

The fifth and final task was a temperament task designed to measure the dog's startle response (Bray et al., 2020). A treat was placed in a bowl. An umbrella was opened and dropped in between the bowl and the dog. The dog's behavior was observed for 30 seconds, during which it could choose to approach the food, interact with the umbrella, or withdraw, while both humans remained neutral.

For tasks that required a choice, dogs were given 30 seconds to make a choice. If no choice was made during that time, the trial was reset. If dogs made no choice for three consecutive trials, a short break was given. If the dog still did not choose on the subsequent trial, then the testing session was aborted.

Data analysis

The cognitive task outcomes for each trial were either binary (e.g., success or failure on a trial) or proportional (e.g., the proportion of the trial in which eye contact was made). Therefore, we used binomial generalized linear mixed models (GLMMs) to evaluate the influence of key variables on task performance. GLMMs model the log odds of a particular outcome and are well-suited for accounting for repeated measures and non-independence of observations by incorporating random effects. Since most tasks involved multiple trials per dog, we included dog identity as a random effect to account for within-subject variability across trials. To account for potential learning or fatigue effects over time, trial number was included as a fixed effect in all models. The main variables of interest, derived from the surveys (MCPQ-R and C-BARQ$^{(S)}$) and dog park behavioral observations, were included as fixed effect predictors. For the pointing task, which had three distinct versions (direct pointing, cross-body pointing, and misleading pointing), task version was included as an additional fixed effect to control for variation in task difficulty. Data analyses were conducted using R statistical software, version 4.3.2 (R Core Team, 2023).

Results

The pointing task was intended to assess the communicative ability of dogs by measuring whether or not they would follow human gestures to locate hidden food rewards. As there were three versions of this task (arm extended towards cup, arm pointing across torso towards cup, and arm extended towards incorrect cup after dog saw correct location), the task version was included as a fixed effect predictor, as well as the survey scores and trial number as fixed effects and the dog identity as a random effect. When the MCPQ-R personality dimension of amicability (i.e., ratings of the dog as more easy-going, friendly, non-aggressive, relaxed, and sociable) was included in the model as a predictor, it was not significantly associated with task performance ($\beta = -0.005$, $p = 0.777$). In contrast, the task version was significantly associated with the odds of following the pointing gesture, with cross-body pointing ($\beta = -1.379$, $p = 6.09\times10^{-7}$) and pointing to the incorrect cup ($\beta = -2.941$, $p < 2\times10^{-16}$) being associated with lower odds of following the gesture than the extended arm pointing. There was no significant effect of trial number ($\beta = 0.031$, $p = 0.321$). When a rating of how communicative the dog is on a scale of 1 to 6 was used as a predictor instead of the MCPQ-R score, the communicative rating was not a significant predictor ($\beta = 0.177$, $p = 0.388$). The effects of task version and trial were consistent with the previous analysis (cross-body pointing: $\beta = -1.387$, $p = 6.81\times10^{-7}$; incorrect cup pointing: $\beta = -2.904$, $p < 2\times10^{-16}$; trial number: $\beta = 0.024$, $p = 0.460$).

Dogs' performance on the pointing task was also analyzed in relation to the observed behavior of the dog in the dog park. It was predicted that dogs that better understood human gestures would perform more play-initiation behaviors in the dog park to communicate with others or would spend more time in proximity to others due to a greater social interest. This was analyzed in the same manner described before. When the frequency of play-initiation behaviors was included in the model, play-initiation behavior was not a significant predictor of performance on the pointing task ($\beta = 0.011$, $p = 0.318$). The effects of task version and trial number were consistent with the analysis of the survey (cross-body pointing: $\beta = -1.397$, $p = 4.84\times10^{-7}$; incorrect cup pointing: $\beta = -2.940$, $p < 2\times10^{-16}$; trial number: $\beta = 0.031$, $p = 0.337$). When the analysis was run with the proportion of time spent within 1 m of other humans or dogs as a predictor, the time spent with others was not significantly associated with pointing task performance ($\beta = -0.678$, $p = 0.648$). As before, task version had a significant effect and trial did not (cross-body pointing: $\beta = -1.382$, $p = 5.88\times10^{-7}$; incorrect cup pointing: $\beta = -2.925$, $p < 2\times10^{-16}$; trial number: $\beta = 0.031$, $p = 0.336$).

For the inhibitory control cylinder task, the outcome of interest was whether or not dogs touched the transparent surface of the cylinder before acquiring the treat. The MCPQ-R dimension of training focus (rating the dog as more attentive, biddable, intelligent, obedient, reliable, and trainable) was predicted to be associated with higher self-control and therefore lower odds of touching the cylinder. Surprisingly, the model with training focus and trial number found that training focus was significantly associated with a greater chance of touching the cylinder ($\beta = 0.026$, $p < 2\times10^{-16}$) and that successive trials were associated with lower chances of touching the cylinder ($\beta = -0.184$, $p < 2\times10^{-16}$). When a 1 through 6 rating of the dog as impulsive was used as the predictor, the rating of impulsivity was not associated with odds of touching the cylinder ($\beta = -0.430$, $p = 0.196$), unlike trial number ($\beta = -0.183$, $p = 0.023$).

For the impossible task, it was predicted that a greater proportion of eye contact would indicate a more socially interested and communicative dog, and thus that it would be associated with the MCPQ-R dimension of amicability or with a rating of the dog being communicative. The model with amicability rating and trial number found no effect of either (amicability: $\beta = -0.044$, $p = 0.174$; trial number: $\beta = 0.500$, $p = 0.137$). When the rating of the dog’s communicativeness was analyzed, contrary to predictions, it was negatively associated with the proportion of eye contact ($\beta = -0.744$, $p = 0.042$) after controlling for trial number ($\beta = 0.510$, $p = 0.133$).

The memory task where the dog had to remember the location of a treat under a cup was predicted to be associated with the MCPQ-R dimension of training focus or negatively associated with descriptions of the dog as forgetful. Training focus was not a significant predictor of the odds of the dog choosing correctly in the memory task ($\beta = 0.048$, $p = 0.072$) after controlling for trial number ($\beta = -0.061$, $p = 0.833$). Ratings of the dog as forgetful were also not associated with memory task performance ($\beta = 0.397$, $p = 0.384$) after controlling for trial number ($\beta = -0.072$, $p = 0.806$).

The umbrella temperament task was designed to measure the fearfulness of dogs by testing whether or not they would consume a treat after an umbrella was unexpectedly opened and dropped in front of them. We predicted that higher MCPQ-R ratings of neuroticism (i.e., rating the dog as more fearful, nervous, submissive, and timid) would correspond to lower odds of eating the food in this task, but there was no association ($\beta = -0.013$, $p = 0.482$). We predicted that dogs that ate the food would score lower on the C-BARQ dimension of fear and anxiety, but there was also no effect ($\beta = -1.34$, $p = 0.145$). It was expected that higher frequency of stress behaviors in the dog park would be associated with lower odds of eating the food, but no significant association was detected ($\beta = -0.060$, $p = 0.707$).

To assist in the interpretation of these results, we conducted a power analysis to estimate the probability of detecting effects of various sizes using binomial linear mixed models with the individual as a random effect (Figure 4-2). We varied the number of trials per individual to include the number of trials for the tasks in this study (namely, one, four, ten, and thirty). As expected, the statistical power increases with larger effect sizes, larger sample sizes of individuals, and larger numbers of trials per individual. With one trial (such as the umbrella temperament task), even quite large effects have a low chance of being detected with the sample size of this study. There is enough power to detect fairly large effects with four trials (e.g., the memory task and impossible task). Ten trials (e.g., the inhibitory control cylinder task, as well as the pointing task for dogs who participated before the more difficult versions of pointing were added) gives quite high power for moderate effects and begins to be more likely to detect more modest effects. Thirty trials (e.g., the pointing task for dogs who completed all versions of the task) allows the detection of all but the smallest effects at the sample sizes in this study.

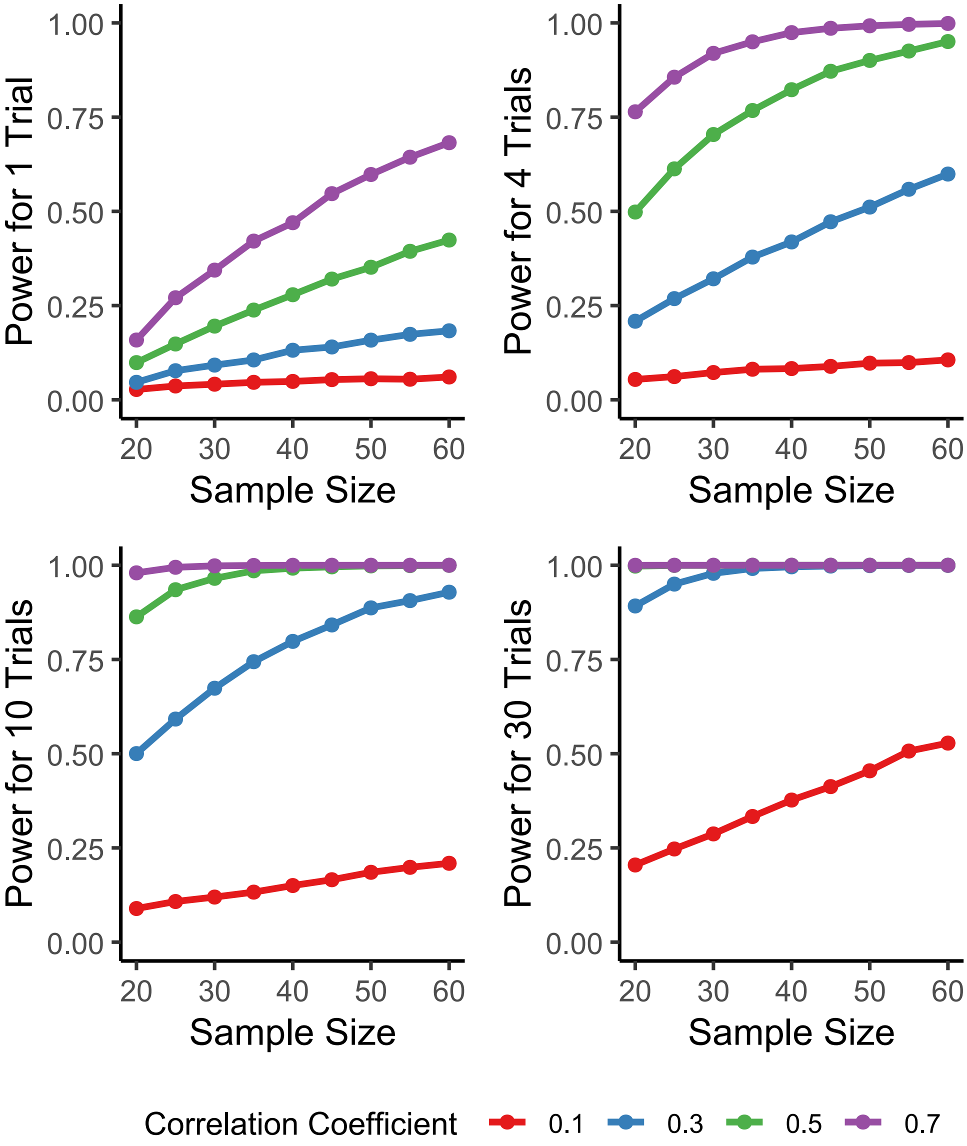

Figure **4-2**: Power analysis for detecting the relationship of a binomial response variable (with varying numbers of trials per individual) to a normally distributed predictor variable. Binomial linear mixed models were used with random effects variables. Correlation represents the relationship between the predictor and the log-odds.

Discussion

In this study, we sought to explore the relationship between dogs' cognition as measured in laboratory tasks with their real-world behavior. Real-world behavior was observed directly in the dog park, where dogs were free to make choices with minimal constraints, providing a more naturalistic context for assessing their social and behavioral tendencies. Additionally, behavior was evaluated through owner-reported surveys, including the validated MCPQ-R and C-BARQ$^{(S)}$, as owners often have unique insights into their dogs' behavior due to their ongoing interactions and daily observations—insights that may not be fully captured in short observational sessions or laboratory tasks. The cognitive tasks were chosen because they represent different domains of dog cognition (Stewart et al., 2015) or have been used in attempts to answer questions regarding domestication (Miklósi et al., 2003; Salomons et al., 2021) and the selection of working dogs (MacLean & Hare, 2018).

Overall, we did not find strong support for our predictions that survey-reported behaviors, performance on cognitive traits, and observed behaviors would correlate. Most survey measures and all dog park observation measures were not significantly associated with cognitive task performance. In some cases, survey ratings were significantly associated with task performance in the opposite direction of what we predicted. For example, we anticipated that dogs rated higher on the MCPQ-R dimension of training focus would be less likely to touch the cylinder in the inhibitory control task, as dogs who fail to inhibit their impulse to reach the food might touch the cylinder rather than taking the necessary detour. However, the opposite was true: dogs rated higher on training focus were significantly more likely to touch the cylinder. The creators of the MCPQ-R survey found that ratings of dogs as attentive, biddable, intelligent, obedient, reliable, and trainable clustered together into a dimension they called training focus (Ley et al., 2008). We initially reasoned that dogs with greater self-control would be rated as more obedient and trainable by their owners, suggesting a link between self-control and the ability to follow training. However, our findings suggest that dogs who were more food-driven or motivated might have rushed towards the treat, indicating a higher level of food motivation rather than a lack of self-control. This interpretation aligns with unexpected findings from other studies, such as the observation that dogs with a tendency to eat feces are often more successful as working dogs (Bray et al., 2019), which may indicate a voracious appetite (Hare & Woods, 2024). Another surprising finding was that dogs rated as more communicative made less eye contact during the impossible task. A possible explanation could be that eye contact on this task may reflect less motivation to solve the task independently more than it reflects communication, and perhaps dogs that are better at communication interpret the task as the experimenter asking them to solve it.

The results regarding the different versions of the pointing task align with expectations. Three versions of the task were used with different levels of difficulty intended to allow greater power to differentiate between dogs. As predicted, the extended arm pointing task had higher odds of success than the cross-body arm pointing version, and the version of the task where the incorrect cup was indicated had the lowest odds of following the gesture. Past research has found that dogs as a whole have a high rate of following a pointing gesture with the arm fully extended (Stewart et al., 2015). This indicates that a more challenging version of the task, such as cross-body pointing or pointing contrasted with memory, may be useful in situations where the goal is to distinguish between individual dogs, as the extended arm pointing may suffer from a ceiling effect that makes it more challenging to distinguish individual performance.

As for the cylinder task, the trial number effect is noteworthy. Dogs becoming less likely to touch the cylinder as trials progressed suggests that they were learning from the task. Dogs likely learn the required detour over time, indicating that they are capable of adapting their behavior to complete the task more effectively with practice. This learning effect underscores the importance of accounting for trial number in studies of cognitive tasks to avoid biasing results by performance improvements due to experience. Future studies might control for this effect either by including trial number as a predictor in statistical models or by analyzing only the first trial to get an untainted measure of initial performance. These task-specific insights suggest that task design, and especially the complexity of the tasks, has a significant impact on how dogs perform, and a nuanced understanding of these effects can help refine future studies.

The lack of significant effects observed in this study could be interpreted in several ways. One possibility is that there may indeed be no strong relationship between the measured cognitive traits and real-world behaviors. Alternatively, it could also mean that the effects are too weak for the current study's sample size and statistical power to detect. A power analysis is a calculation of the probability of a statistically significant result being detected under certain conditions, typically a particular population effect size and sample size (Quach et al., 2022). Power analyses are typically done before a study is conducted in order to ensure that the study is realistically equipped to be likely to find an effect of a particular magnitude deemed practically meaningful (Quach et al., 2022). However, in some cases, post hoc power analyses are done after a study is conducted in order to clarify null results to help interpret the size of the effect that could have been detected (Quach et al., 2022; Zhang et al., 2019). Post hoc power analyses have come under criticism for being conceptually flawed, as statistical power is the probability of an event that has not yet occurred, but after an analysis is conducted, the results have already occurred (Quach et al., 2022). The most common mistake of post hoc analyses is using the effect size from the sample as a stand-in for the effect size of the whole population (Quach et al., 2022). While the effect size from the sample is in many cases the best available estimate of the population effect size, it can be widely different, especially when the sample size is low, and simulation studies indicate that this practice can yield very misleading power estimates (Quach et al., 2022; Zhang et al., 2019). In this study, the power analysis was conducted post hoc. However, to minimize the problem described above, we did not use the effect sizes from the sample, instead estimating the power based on a variety of possible population effect sizes in a manner similar to what can be done in a prospective power analysis. The power analysis indicates the pointing task likely had the most statistical power out of the tasks in this study, followed by the inhibitory control task, the unsolvable task and memory task, and finally the umbrella temperament task. With this in mind, the lack of significant associations with the umbrella temperament task are unsurprising. We do not think it is likely that this null result indicates a lack of an effect, nor are the lack of effects from the unsolvable task and memory task likely to indicate an absence of a small or moderate effect. However, a moderate association with the pointing task would have been likely to be detected in this study, so we are more confident in the assertion that this represents a lack of an association.

Despite the absence of robust associations in this study, the link between certain cognitive tasks and real-world outcomes in other contexts, such as the success or failure of working dogs, supports the idea that these tasks may have practical relevance in specific situations. For example, gesture comprehension and memory tasks have been shown to predict the success of military detection dogs (MacLean & Hare, 2018). This suggests that there is indeed a connection between cognitive abilities and practical behaviors, even if this connection was not fully captured in the current study. It is possible that the traits measured by the cognitive tasks, observations, and surveys may not align well in this particular dataset, given the differences in the specific domains they assess. For example, the umbrella task, which was designed to measure fearfulness through the dog’s response to a startling event, might tap into a very specific domain of fear that does not necessarily correspond to the more general or everyday fearfulness rated by owners or observed in the dog park. This suggests that not all cognitive tasks are equally predictive of the broader behavioral tendencies assessed in the surveys or observed in the natural environment. Similarly, gesture comprehension and play-initiation behaviors may reflect different aspects of a dog’s communication abilities. Dogs that excel at comprehending human gestures might not necessarily engage more in social play, indicating that different cognitive or behavioral domains do not always correlate strongly.

This research is relevant to our understanding of not just dog cognition but also the cognition of humans and other species. In some ways, humans' social cognition is more similar to dogs than to even chimpanzees, as dogs are more successful at following human gestures than chimpanzees are (Hare et al., 2002), and the structure of individual differences is more similar between human infants and dogs (with social and non-social cognitive tasks clustering together) than to chimpanzees (MacLean et al., 2017). Some have proposed that the cognitive similarities of dogs and humans are the result of convergent selective pressures against aggression, termed the human self-domestication hypothesis (Hare, 2017). This study did not find evidence that the gesture comprehension task was associated with dogs' broader communicative ability. However, in Chapter 3, we found associations between gesture comprehension and survey questions about dogs' communicative behavior. These distinctions can help clarify what is being measured by this task and how it may be relevant to human cognition. For instance, Chapter 3 showed that gesture comprehension in dogs was linked to the number of words known, but this chapter found no link to play-initiating behaviors in the dog park. This suggests possible relevance of this task to abilities like language, while implying that specific usage of this ability in situations like play may be influenced by other factors such as interest in others and the specific social environment. One finding of this study was that the cylinder task was associated with training focus in the opposite of the predicted direction, with dogs rated as higher in training focus being more likely to touch the cylinder. This finding also helps with the interpretation of other research on the cognition of humans and other species. Across a wide range of mammals and birds, species with lower rates of touching the cylinder have larger brains (MacLean et al., 2014) and more cortical neurons (Herculano-Houzel, 2017). This has been used as evidence to argue that the evolutionary increases in human brain size indicate high levels of self-control (Hare, 2017). However, as this task may be confounded by varying levels of motivation, caution should be taken in interpreting results of this task across species.

Future research should continue to examine the cognitive tasks described in this study to better understand how well they correspond with real-world dog behavior. As citizen science has proven more effective at detecting these small effects (Chapter 3), it could be worthwhile to explore the inhibitory control, impossible task, and umbrella task in a future citizen science project. By utilizing a broad volunteer network, researchers could gather more data, increasing the ability to detect smaller but meaningful relationships between cognition and behavior. Another promising approach to address the issue of small effect sizes is through multi-lab collaborations such as the ManyDogs project, which facilitates large-scale data collection across multiple research labs (ManyDogs Project et al., 2023). By pooling data from various dog cognition laboratories, it becomes possible to amass larger sample sizes, which would provide greater statistical power to detect relationships between cognitive tasks and dog behavior. Such collaborations could also help create more standardized protocols for measuring cognitive tasks, increasing the consistency and comparability of results. Additionally, it may be helpful to develop and validate a comprehensive survey that specifically assesses a wide variety of dog behaviors, which could provide more granular insights into how specific behaviors relate to cognitive performance. Current surveys like the MCPQ-R or the C-BARQ might not capture all of the behavioral domains measured by the cognitive tasks, suggesting that a more tailored survey could improve our understanding of the relationship between cognitive abilities and real-world behavior.

This study's findings suggest that the inhibitory control task may be more sensitive to motivation than previously assumed. Dogs that are highly motivated by food might perform differently from dogs that are less motivated, influencing their performance on this task. Therefore, future studies using the cylinder task should consider potential trial effects, especially given that dogs learn over repeated trials, which could confound the results. Researchers may also want to account for motivation levels in their analyses, perhaps including measures of food motivation or training focus to help interpret the results more accurately. Finally, the study recommends that researchers conducting gesture comprehension studies consider using more challenging versions of the task than the standard extended arm pointing task. While this version may provide insights into dog cognition, its simplicity could result in a ceiling effect, limiting the ability to distinguish between individual dogs. By using more complex tasks, such as cross-body pointing or tasks that require memory, researchers can better differentiate dogs' abilities and capture more subtle variations in cognition. In conclusion, future studies should build upon the groundwork laid by this research, exploring the connection between cognitive tasks and real-world behavior with larger samples, more tailored surveys, and more challenging task versions. Through collaboration and innovation, the understanding of dog cognition can be significantly advanced.

References

Ameen, C., Feuerborn, T. R., Brown, S. K., Linderholm, A., Hulme-Beaman, A., Lebrasseur, O., Sinding, M. H. S., Lounsberry, Z. T., Lin, A. T., Appelt, M., Bachmann, L., Betts, M., Britton, K., Darwent, J., Dietz, R., Fredholm, M., Gopalakrishnan, S., Goriunova, O. I., Grønnow, B., … Evin, A. (2019). Specialized sledge dogs accompanied Inuit dispersal across the North American Arctic. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1916). https://doi.org/10.1098/rspb.2019.1929

Balme, J., O'Connor, S., & Fallon, S. (2018). New dates on dingo bones from Madura Cave provide oldest firm evidence for arrival of the species in Australia. *Scientific Reports*, *8*(1), 4–9. https://doi.org/10.1038/s41598-018-28324-x

Bergström, A., Frantz, L., Schmidt, R., Ersmark, E., Lebrasseur, O., Girdland-Flink, L., Lin, A. T., Storå, J., Sjögren, K.-G., Anthony, D., Antipina, E., Amiri, S., Bar-Oz, G., Bazaliiskii, V. I., Bulatović, J., Brown, D., Carmagnini, A., Davy, T., Fedorov, S., … Skoglund, P. (2020). Origins and genetic legacy of prehistoric dogs. *Science*, *370*(557–564), 1–7.

Brady, K., Hewison, L., Wright, H., Zulch, H., Cracknell, N., & Mills, D. (2018). A spatial discounting test to assess impulsivity in dogs. *Applied Animal Behaviour Science*, *202*(July 2017), 77–84. https://doi.org/10.1016/j.applanim.2018.01.003

Bray, E. E., Gruen, M. E., Gnanadesikan, G. E., Horschler, D. J., Levy, K. M., Kennedy, B. S., Hare, B. A., & MacLean, E. L. (2020). Cognitive characteristics of 8-to-10-week-old assistance dog puppies. *Animal Behaviour*, *166*, 193–206. https://doi.org/10.1016/j.anbehav.2020.05.019

Bray, E. E., Levy, K. M., Kennedy, B. S., Duffy, D. L., Serpell, J. A., & MacLean, E. L. (2019). Predictive models of assistance dog training outcomes using the Canine Behavioral Assessment and Research Questionnaire and a standardized temperament evaluation. *Frontiers in Veterinary Science*, *6*(49), 1–11. https://doi.org/10.3389/fvets.2019.00049

Chambers, J., Quinlan, M. B., Evans, A., & Quinlan, R. J. (2020). Dog-human coevolution: cross-cultural analysis of multiple hypotheses. *Journal of Ethnobiology*, *40*(4), 414–433. https://doi.org/10.2993/0278-0771-40.4.414

Coppinger, L., & Coppinger, R. (2000). Dogs for herding and guarding livestock. In T. Grandin (Ed.), *Livestock Handling and Transport* (2nd ed., pp. 235–253).

Freedman, A. H., & Wayne, R. K. (2017). Deciphering the origin of dogs: from fossils to genomes. *Annual Review of Animal Biosciences*, *5*(1), 281–307. https://doi.org/10.1146/annurev-animal-022114-110937

Friard, O., & Gamba, M. (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution*, *7*(11), 1325–1330. https://doi.org/10.1111/2041-210X.12584

Greig, K., Boocock, J., Allen, M. S., Matisoo-Smith, L., & Walter, R. (2018). Ancient DNA evidence for the introduction and dispersal of dogs (Canis familiaris) in New Zealand. *Journal of Pacific Archaeology*, *9*(1), 1–10.

Guagnin, M., Perri, A. R., & Petraglia, M. D. (2018). Pre-Neolithic evidence for dog-assisted hunting strategies in Arabia. *Journal of Anthropological Archaeology*, *49*(November 2017), 225–236. https://doi.org/10.1016/j.jaa.2017.10.003

Hall, N. J., Johnston, A. M., Bray, E. E., Otto, C. M., MacLean, E. L., & Udell, M. A. R. (2021). Working dog training for the twenty-first century. *Frontiers in Veterinary Science*, *8*(July), 1–18. https://doi.org/10.3389/fvets.2021.646022

Hare, B. (2017). Survival of the friendliest: Homo sapiens evolved via selection for prosociality. *Annual Review of Psychology*, *68*(1), 155–186. https://doi.org/10.1146/annurev-psych-010416-044201

Hare, B., Brown, M., Williamson, C., & Tomasello, M. (2002). The domestication of social cognition in dogs. *Science*, *298*(5598), 1634–1636. https://doi.org/10.1126/science.1072702

Hare, B., & Ferrans, M. (2021). Is cognition the secret to working dog success? *Animal Cognition*, *24*(2), 231–237. https://doi.org/10.1007/s10071-021-01491-7

Hare, B., Plyusnina, I., Ignacio, N., Schepina, O., Stepika, A., Wrangham, R., & Trut, L. (2005). Social cognitive evolution in captive foxes is a correlated by-product of experimental domestication. *Current Biology*, *15*, 226–230. https://doi.org/10.1016/j

Hare, B., & Woods, V. (2024). *Puppy Kindergarten: the new science of raising a great dog* (First). Random House, LLC.

Herculano-Houzel, S. (2017). Numbers of neurons as biological correlates of cognitive capability. *Current Opinion in Behavioral Sciences*, *16*, 1–7.

Koungoulos, L., & Fillios, M. (2020). Hunting dogs down under? On the Aboriginal use of tame dingoes in dietary game acquisition and its relevance to Australian prehistory. *Journal of*

Anthropological Archaeology, *58*(September 2019), 101146. https://doi.org/10.1016/j.jaa.2020.101146

Ley, J. M., Bennett, P. C., & Coleman, G. J. (2008). A refinement and validation of the Monash Canine Personality Questionnaire (MCPQ). *Applied Animal Behaviour Science*, *116*, 220–227. https://doi.org/10.1016/j.applanim.2008.09.009

Lupo, K. D. (2019). Hounds follow those who feed them: What can the ethnographic record of hunter-gatherers reveal about early human-canid partnerships? *Journal of Anthropological Archaeology*, *55*(April), 101081. https://doi.org/10.1016/j.jaa.2019.101081

MacLean, E. L., & Hare, B. (2018). Enhanced selection of assistance and explosive detection dogs using cognitive measures. *Frontiers in Veterinary Science*, *5*(236), 1–14. https://doi.org/10.3389/fvets.2018.00236

MacLean, E. L., Hare, B., Nunn, C. L., Addessi, E., Amici, F., Anderson, R. C., Aureli, F., Baker, J. M., Bania, A. E., Barnard, A. M., Boogert, N. J., Brannon, E. M., Bray, E. E., Bray, J., Brent, L. J. N., Burkart, J. M., Call, J., Cantlo, J. F., Chek, L. G., … Zhao, Y. (2014). The evolution of self-control. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(20). https://doi.org/10.1073/pnas.1323533111

MacLean, E. L., Herrmann, E., Suchindran, S., & Hare, B. (2017). Individual differences in cooperative communicative skills are more similar between dogs and humans than chimpanzees. *Animal Behaviour*, *126*, 41–51. https://doi.org/10.1016/j.anbehav.2017.01.005

MacLean, E. L., Matthews, L. J., Hare, B. A., Nunn, C. L., Anderson, R. C., Aureli, F., Brannon, E. M., Call, J., Drea, C. M., Emery, N. J., Haun, D. B. M., Herrmann, E., Jacobs, L. F., Platt, M. L., Rosati, A. G., Sandel, A. A., Schroepfer, K. K., Seed, A. M., Tan, J., … Wobber, V. (2012). How does cognition evolve. *Animal Cognition*, *15*(2), 223–238. https://doi.org/10.1007/s10071-011-0448-8.How

ManyDogs Project, Alberghina, D., Bray, E. E., Buchsbaum, D., Byosiere, S. E., Espinosa, J., Gnanadesikan, G. E., Guran, C. N. A., Hare, E., Horschler, D. J., Huber, L., Kuhlmeier, V. A., MacLean, E. L., Pelgrim, M. H., Perez, B., Ravid-Schurr, D., Rothkoff, L., Sexton, C. L., Silver, Z. A., & Stevens, J. R. (2023). ManyDogs Project: a big team science approach to investigating canine behavior and cognition. *Comparative Cognition and Behavior Reviews*, *18*, 59–77. https://doi.org/10.3819/CCBR.2023.180004

McPeake, K. J., Collins, L. M., Zulch, H., & Mills, D. S. (2021). Behavioural and physiological correlates of the Canine Frustration Questionnaire. *Animals*, *11*(3346), 1–15.

Miklósi, Á. (2015). *Dog behaviour, evolution, and cognition* (2nd ed.). Oxford University Press.

Miklósi, Á., Kubinyi, E., Topál, J., Gácsi, M., Virányi, Z., & Csányi, V. (2003). A simple reason for a big difference: Wolves do not look back at humans, but dogs do. *Current Biology*, *13*(13), 763–766. https://doi.org/10.1016/S

Mongillo, P., Scandurra, A., Eatherington, C. J., D'Aniello, B., & Marinelli, L. (2019). Development of a spatial discount task to measure impulsive choices in dogs. *Animals*, *9*(7), 1–14. https://doi.org/10.3390/ani9070469

Ottenheimer Carrier, L., Cyr, A., Anderson, R. E., & Walsh, C. J. (2013). Exploring the dog park: Relationships between social behaviours, personality and cortisol in companion dogs. *Applied Animal Behaviour Science*, *146*(1–4), 96–106. https://doi.org/10.1016/j.applanim.2013.04.002

Perri, A. R. (2020). Prehistoric dogs as hunting weapons: the advent of animal biotechnology. In B. Berthke & A. Burtt (Eds.), *Dogs: Archaeology of the Human-Canine Connection Beyond Domestication* (pp. 7–44). University Press of Florida.

Perri, A. R., Feuerborn, T. R., Frantz, L. A. F., Larson, G., & Malhi, R. S. (2021). Dog domestication and the dual dispersal of people and dogs into the Americas. *Proceedings of the National Academy of Sciences*, *118*(6), 1–8. https://doi.org/10.1073/pnas.2010083118

Pew Research Center. (2006). Gauging family intimacy: dogs edge cats (dads trail both). In *Pew Research Center: A Social Trends Report*.

Pitulko, V. V., & Kasparov, A. K. (2017). Archaeological dogs from the Early Holocene Zhokhov site in the Eastern Siberian Arctic. *Journal of Archaeological Science: Reports*, *13*(May), 491–515. https://doi.org/10.1016/j.jasrep.2017.04.003

Quach, N. E., Yang, K., Chen, R., Tu, J., Xu, M., Tu, X. M., & Zhang, X. (2022). Post-hoc power analysis: a conceptually valid approach for power based on observed study data. *General Psychiatry*, *35*(4), 1–7. https://doi.org/10.1136/gpsych-2022-100764

R Core Team. (2023). *R: a language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.r-project.org

Rosati, A. G. (2017). Foraging cognition: reviving the ecological intelligence hypothesis. *Trends in Cognitive Sciences*, *21*(9), 691–702. https://doi.org/10.1016/j.tics.2017.05.011

Saavedra-Aracena, L., Grimm-Seyfarth, A., & Schüttler, E. (2021). Do dog-human bonds influence movements of free-ranging dogs in wilderness? *Applied Animal Behaviour Science*, *241*(April), 105358. https://doi.org/10.1016/j.applanim.2021.105358

Salomons, H., Smith, K. C. M., Callahan-Beckel, M., Callahan, M., Levy, K., Kennedy, B. S., Bray, E. E., Gnanadesikan, G. E., Horschler, D. J., Gruen, M., Tan, J., White, P., VonHoldt, B. M., MacLean, E. L., & Hare, B. (2021). Cooperative communication with humans evolved to emerge early in domestic dogs. *Current Biology*, *31*(July), 1–8. https://doi.org/10.1016/j.cub.2021.06.051

Shannon, L. M., Boyko, R. H., Castelhano, M., Corey, E., Hayward, J. J., McLean, C., White, M. E., Said, M. A., Anita, B. A., Bondjengo, N. I., Calero, J., Galov, A., Hedimbi, M., Imam, B., Khalap, R., Lally, D., Masta, A., Oliveira, K. C., Pérez, L., … Boyko, A. R. (2015). Genetic structure in village dogs reveals a Central Asian domestication origin. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(44), 13639–13644. https://doi.org/10.1073/pnas.1516215112

Shettleworth, S. J. (2001). Animal cognition and animal behaviour. *Animal Behaviour*, *61*(2), 277–286. https://doi.org/10.1006/anbe.2000.1606

Shettleworth, S. J. (2010). *Cognition, evolution, and behavior* (2nd ed.). Oxford University Press.

Stevens, J. R., Mathias, M., Herridge, M., Hughes-Duvall, K., Wolff, L. M., & Yohe, M. (2022). Do owners know how impulsive their dogs are? *Animal Behavior and Cognition*, *9*(3), 261–286.

Stewart, L., MacLean, E. L., Ivy, D., Woods, V., Cohen, E., Rodriguez, K., McIntyre, M., Mukherjee, S., Call, J., Kaminski, J., Miklósi, Á., Wrangham, R. W., & Hare, B. (2015). Citizen science as a new tool in dog cognition research. *PLoS ONE*, *10*(9), 1–16. https://doi.org/10.1371/journal.pone.0135176

Svartberg, K. (2005). A comparison of behaviour in test and in everyday life: Evidence of three consistent boldness-related personality traits in dogs. *Applied Animal Behaviour Science*, *91*(1–2), 103–128. https://doi.org/10.1016/j.applanim.2004.08.030

Thalmann, O., Shapiro, B., Cui, P., Schuenemann, V. J., Sawyer, S. K., Greenfield, D. L., Germonpré, M. B., Sablin, M. V., López-Giráldez, F., Domingo-Roura, X., Napierala, H., Uerpmann, H.-P., Loponte, D. M., Acosta, A. A., Giemsch, L., Schmitz, R. W., Worthington, B., Buikstra, J. E., Druzhkova, A., … Wayne, R. K. (2013). Complete mitochondrial genomes of ancient canids suggest a European origin of domestic dogs. *Science*, *342*(November), 871–874.

Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift Für Tierpsychologie*, *20*, 410–433.

Trut, L., Oskina, I., & Kharlamova, A. (2009). Animal evolution during domestication: the domesticated fox as a model. *Bioessays*, *31*(3), 349–360. https://doi.org/10.1038/jid.2014.371

Wang, G. D., Zhai, W., Yang, H. C., Wang, L., Zhong, L., Liu, Y. H., Fan, R. X., Yin, T. T., Zhu, C. L., Poyarkov, A. D., Irwin, D. M., Hytönen, M. K., Lohi, H., Wu, C. I., Savolainen, P., & Zhang, Y. P. (2016). Out of southern East Asia: The natural history of domestic dogs across the world. *Cell Research*, *26*(1), 21–33. https://doi.org/10.1038/cr.2015.147

Welker, M. H., & Byers, D. A. (2019). The birch creek canids and dogs as transport labor in the intermountain west. *American Antiquity*, *84*(1), 88–106. https://doi.org/10.1017/aaq.2018.81

Wilkins, A. S., Wrangham, R. W., & Tecumseh Fitch, W. (2014). The “domestication syndrome” in mammals: A unified explanation based on neural crest cell behavior and genetics. *Genetics*, *197*(3), 795–808. https://doi.org/10.1534/genetics.114.165423

Wilkins, V., Evans, J., Park, C., Fitzpatrick, A. L., Creevy, K. E., & Ruple, A. (2024). Validation of the shortened version of the Canine Behavioral Assessment and Research Questionnaire (C-BARQ) using participants from the Dog Aging Project. *PLoS ONE*, *19*(4 April), 1–15. https://doi.org/10.1371/journal.pone.0299973

Zhang, Y., Hedo, R., Rivera, A., Rull, R., Richardson, S., & Tu, X. M. (2019). Post hoc power analysis: is it an informative and meaningful analysis? *General Psychiatry*, *32*(4), 3–6. https://doi.org/10.1136/gpsych-2019-100069

Chapter 5

Rethinking Cortisol as a Measure of Stress in Dogs: Insights from Salivary and Hair Samples

Introduction

Animals respond to stressors by activating neuroendocrine pathways that trigger a coordinated bodily response that prioritizes the most pressing bodily functions needed to handle the stressful situation (O’Connor et al., 2021). One stress system, the sympathetic-adrenal-medullary (SAM) system, initiates a cascade from the amygdala to the hypothalamus to the adrenal glands, causing the release of noradrenaline. Within seconds, this prepares the body to respond to the stressor by increasing breathing and heart rates, dilating the pupils, and decreasing digestive function to redirect blood flow to the muscles instead (O’Connor et al., 2021). Simultaneously, another stress system, the hypothalamic-pituitary-adrenal (HPA) axis, triggers a cascade of hormone releases, ultimately causing the adrenal cortex to release cortisol, a glucocorticoid hormone. Cortisol mobilizes energy in the form of glucose for use by the muscles and the brain while also reducing inflammation (O’Connor et al., 2021). Beyond its roles in stress, cortisol also helps regulate other critical functions such as circadian rhythms (O’Connor et al., 2021). These stress responses serve adaptive functions by enabling individuals to allocate energy in an effective manner to address the immediate threat, thereby increasing their chances of survival and reproduction in the long term (Boonstra, 2013; O’Connor et al., 2021).

Changes to the stress response are believed to be critical to animal domestication. One of the most important and universal traits of domesticated animals is their reduced fear of humans compared to their wild progenitors (Sánchez-Villagra et al., 2016; Zeder, 2012). For example, while dog puppies and wolf pups are equally likely to approach a familiar object, wolf pups are significantly more likely to avoid humans and unfamiliar objects, with the greatest difference observed in their response to unfamiliar humans (Salomons et al., 2021). Genes that are highly differentiated between dogs and wolves are particularly likely to be involved in the adrenaline and noradrenaline biosynthesis pathway, which is part of the SAM system stress response (Cagan & Blass, 2016). These findings highlight the importance of reduced fear responses in dogs as a result of domestication. Experimental studies of domestication further support this idea. Since the 1950s, Russian biologists, directed first by Dmitry Belyaev and later by Lyudmila Trut, have selectively bred red foxes in an effort to mimic dog domestication (Trut et al., 2004, 2009). Foxes raised with minimal human contact were tested for their responses to humans and selectively bred for tameness. Remarkably, within just a few generations, these foxes no longer exhibited fear of humans (Trut et al., 2009). The HPA axis and glucocorticoids are believed to play critical roles in this process. In fox pups, the end of the socialization period, the time when they can become accustomed to new stimuli without fear, is marked by a rise in plasma cortisol concentrations. In domesticated foxes, however, this rise occurs later than in control foxes (Trut et al., 2009). After 45 generations of selection, plasma cortisol concentrations were three times lower in domesticated foxes than in controls, and when under stress, five times lower (Trut et al., 2009). The shared traits observed across domesticated animals, including these foxes, have been proposed to result from developmental changes that affect the adrenal glands, as well as other features of the “domestication syndrome” (A. S. Wilkins et al., 2014). Since cortisol regulation and the HPA axis may be central to domestication, fully understanding dog domestication will require the ability to measure cortisol levels in dogs and relate them to their behavioral responses to stimuli.

While the stress response serves an adaptive function in the short-term, chronic stress has been consistently associated with negative long-term health outcomes (O’Connor et al., 2021;

Sapolsky, 2004). High levels of early life adversity are associated with worse chronic health outcomes in various species, but it remains debated whether this results from predictive adaptive responses (i.e., the evolution of plastic development that anticipates the continuation of stressful environments and develops in a way that is optimal for this) or developmental constraints (i.e., optimizing for dealing with the current stressor even if this causes a trade-off resulting in suboptimal outcomes later in life) (Snyder-Mackler et al., 2020). Frequent activation of the stress response can lead to immune dysfunction, characterized by persistent inflammation alongside suppression of other immune functions (O'Connor et al., 2021). The glucocorticoid resistance hypothesis proposes that chronic activation of the HPA axis desensitizes the glucocorticoid receptors of immune cells and results in long-term inflammation (Miller et al., 2002; O'Connor et al., 2021). As a result, health and survival can be negatively impacted by chronic stress. However, the relationship between acute and chronic stress are underexplored (Rohleder, 2019). In pet dogs, chronic stress has been linked to both health and survival outcomes. Dogs that exhibit greater fear of strangers, on average, have shorter lifespans and experience more frequent and severe disease (Dreschel, 2010). Beyond shortening lifespan, chronic stress can also significantly diminish a dog's quality of life (Lamon et al., 2021; Protopopova, 2016).

Because cortisol is released into the bloodstream following HPA axis activation, it has often been used as a biomarker of stress in dogs, humans, and other animals (Cobb et al., 2016; O'Connor et al., 2021). While blood serum cortisol is a more direct physiological measure of stress, salivary cortisol is widely used in dogs because its collection is simpler, less distressing, and has been validated as strongly correlated with serum cortisol (Beerda et al., 1996; Giannetto et al., 2014). With both types of measures, several confounding factors must be considered when conducting measurements. Serum and salivary cortisol levels spike in the morning and subsequently decline throughout the day (Giannetto et al., 2014), so time is an important confounder. Salivary cortisol concentrations have been found to be affected by the dog's sex, neuter status, age, the collection materials, and testing environment (Cobb et al., 2016). Cortisol is also incorporated into hair as it grows (Raul et al., 2004), allowing for the measurement of average cortisol levels over one or more months (O'Connor et al., 2021). However, hair color is an important confounder, as even within the same dog, dark hair tends to have lower hair cortisol concentrations than light hair (Bennett & Hayssen, 2010).

In addition to physiological measures of stress such as cortisol, behavioral measures have also been used to measure stress in dogs. These include direct behavioral observations (e.g., tail tucking or hunched posture) (Ottenheimer Carrier et al., 2013), owner surveys (Ley et al., 2008; V. Wilkins et al., 2024), or laboratory-based tests (Bray et al., 2020; McPeake et al., 2021). Understanding how well these behavioral measures correspond to cortisol levels will enhance both future research using behavioral assessments and studies relying on salivary and hair cortisol in dogs. However, because the stress response is highly complex, both behaviorally and physiologically, it is important to determine the extent to which different measures capture distinct aspects of stress. Given that changes in the stress response, particularly cortisol regulation, are implicated in domestication, validating stress measures is essential for understanding how domestication has shaped the stress response. These insights also have clear implications for dog welfare as accurately measuring stress can help assess the effects of potentially stressful environmental factors and evaluate mitigation strategies. In this study, we analyze salivary and hair cortisol from pet dogs alongside behavioral observations, survey data, and laboratory-based temperament tasks to assess how well these measures correlate. We test whether salivary cortisol and hair cortisol correlate in dogs, and we test whether these cortisol measures correspond to behavioral measures of stress acutely (through observed stress behaviors at the time of saliva sampling) and chronically (through surveying owners about dogs typical behavior and conducting a temperament test).

Methods

Data collection

Pet dogs were recruited from Tudek Dog Park in State College, Pennsylvania, United States. Fifty-six dogs were sampled (30 males and 26 females, with 21 neutered and 23 spayed, respectively). Dogs ranged from just under 4 months to 9 years in age with a median age of 2 years. Breeds were variable and included both purebred and mixed-breed dogs. To establish a baseline measurement of circulating cortisol, saliva was sampled from dogs upon their arrival prior to entering the dog park. A Children's Swab (Salimetrics #5001.06) was placed into the right side of the dog's mouth and swabbed around the cheeks and gums for at least 30 seconds in order to absorb saliva. A treat was held in front of the dog's mouth to stimulate salivation, but the treat was not given until after the saliva had been collected to prevent sample contamination. As the sample was being collected, the dog owner provided basic demographic information and completed the Monash Canine Personality Questionnaire-Revised (MCPQ-R), which asks about the dog's personality, including measures interpreted as neuroticism (Ley et al., 2008). Next, dogs entered the dog park with their owners, who were instructed to act as they normally would at the dog park. The focal dogs were filmed for 30 minutes, with the observer keeping a running count of the number of people and dogs in the park throughout the observation. After the 30 minutes ended, the dog left the park, and a second saliva sample was collected in the manner described above. Saliva samples were placed on ice immediately after collection and then transported to a -20°C freezer for storage.

At a second, lab-based session on a different day (usually within a week), a hair sample was taken upon arrival to measure hair cortisol. The hair sample was cut from the dorsal base of the tail using small scissors sanitized with alcohol, and hair color was recorded as a potential confound. The sample was placed in an envelope and stored at room temperature. Meanwhile, the owner filled out the shortened Canine Behavioral Assessment and Research Questionnaire (C-BARQ$^{(S)}$) to give a more detailed assessment of the dog's behavior in the domain of fear and aggression (V. Wilkins et al., 2024). To assess response to novelty, dogs participated in the umbrella task (Bray et al., 2020). The researcher placed a treat in a bowl while the dog owner sat on a stool behind the dog. The researcher then opened an umbrella towards the dog and dropped it between the bowl and the dog. For 30 seconds, the dog was allowed to respond to this situation freely, including by eating the food and interacting with the umbrella, while the humans maintained neutral postures.

Data processing

The dog park observation videos were later analyzed in the program BORIS (Friard & Gamba, 2016) to quantify instances of stress behaviors in the focal dog, following the ethogram used by Ottenheimer Carrier et al. (Ottenheimer Carrier et al., 2013). Video coding order was randomized using R.

The saliva samples were stored at -20°C and shipped on dry ice to Salimetrics for cortisol analysis. Samples were thawed, vortexed, and then centrifuged at 1,500 g for 15 minutes. Immediately afterwards, they were assayed for cortisol with a high sensitivity enzyme-linked immunosorbent assay (ELISA). Sample test volume was 25 µL of saliva per determination. Assays were performed in duplicate, and the samples from this study were assayed in two batches.

Hair samples were stored at room temperature. The hair samples (n = 50) were shipped to Stress Bioanalytics, LLC, for cortisol analysis following previously published protocols (Blodgett et al., 2017; Vega Ocasio et al., 2021). The 1 cm closest to the root of the hair was trimmed away for samples longer than that length. Hair samples were washed twice with isopropanol, then dried in a 75°C oven, weighed, and milled with stainless steel balls. Cortisol was extracted with methanol overnight, acetone for 5 minutes, with methanol overnight again, and then dried with acetone. The samples were then dissolved into an assay diluent and assayed in duplicate using an ELISA.

Data analysis

We statistically analyzed the relationships between different cortisol measures and between cortisol levels and stress-related behavioral measures. Sample sizes varied across variables, as some dogs did not complete every aspect of the study or had unusable data. Additionally, the C-BARQ survey component was added later in the study. Correlations between continuous variables were assessed using Pearson's product-moment correlation tests. Comparisons of continuous variables across multiple categories were conducted using analysis of variance (ANOVA). For models with multiple predictors—such as predicting final salivary cortisol levels based on baseline salivary cortisol and behavioral measures—linear models were used. For binary or count data, generalized linear models were applied with binomial or Poisson link functions, respectively. All statistical analyses were performed in R statistical software (R Core Team, 2023).

Results

Cortisol distributions

Out of all the pre- and post-dog park salivary cortisol samples, 104 were successfully assayed at least once, and 95 had sufficient saliva for a successful second replicate. Among the 95 samples with two replicates, the replicates were highly correlated (Pearson's product-moment correlation test, $r = 0.9997$, $p < 2.2 \times 10^{-16}$), including after log-transformation (Pearson's product-moment correlation test, $r = 0.9987$, $p < 2.2 \times 10^{-16}$). Given this strong correlation, downstream analyses of salivary cortisol used the average of the two replicates when available and a single value for samples with a single replicate. Salivary cortisol values ranged from 0.055 to 4.796 µg/dL, with a median of 0.241 µg/dL and a mean of 0.529 µg/dL. Due to a significant right-skew in the data (Shapiro-Wilk normality test, $W = 0.558$, $p = 3.57 \times 10^{-16}$), salivary cortisol values were log-transformed for downstream analyses. Since recent studies have identified significant effects of stress interventions when categorizing salivary cortisol as high or low (McPeake et al., 2021), we also classified each value as indicating stress (> 0.4 µg/dL) or no stress (< 0.4 µg/dL). Two post-park cortisol samples had ambiguous labels and were excluded from numerical analyses, but since both fell within the unstressed category, these individuals were included in the categorical analyses. Based on this classification, 29 dogs were unstressed both before and after the dog park, five dogs started as unstressed and became stressed, eight dogs started as stressed and became unstressed, and eight dogs started and ended as stressed.

Out of the 50 hair samples assayed for cortisol, 48 had concentrations below 20 pg/mg, consistent with previously published values for dog hair cortisol (Bennett & Hayssen, 2010). However, two samples exceeded 120 pg/mg, which could be due to the effects of topical glucocorticoids or other medications. Although the survey inquired about drugs the dogs were taking and the outlier dogs were not reported to be taking drugs, these values were nevertheless excluded from downstream analyses. This decision was made because the owners may have omitted or forgotten to mention certain treatments, and such extreme values are unlikely to be naturally occurring. After excluding these outliers, hair cortisol concentration ranged from 3.41 to 19.49 pg/mg, with a median of 8.89 pg/mg and a mean of 9.49 pg/mg. Since hair color has previously reported to affect cortisol uptake into hair, we tested to see whether hair cortisol concentrations differed based on hair color, which would necessitate including this as a confound in models. Hair color was rated ordinally on a three-point scale from following previous work that found an effect of hair color (Bennett & Hayssen, 2010), but no significant differences in cortisol concentration were detected across hair colors (*r* = 0.092, *n* = 48, *p* = 0.536, Figure 5-1).

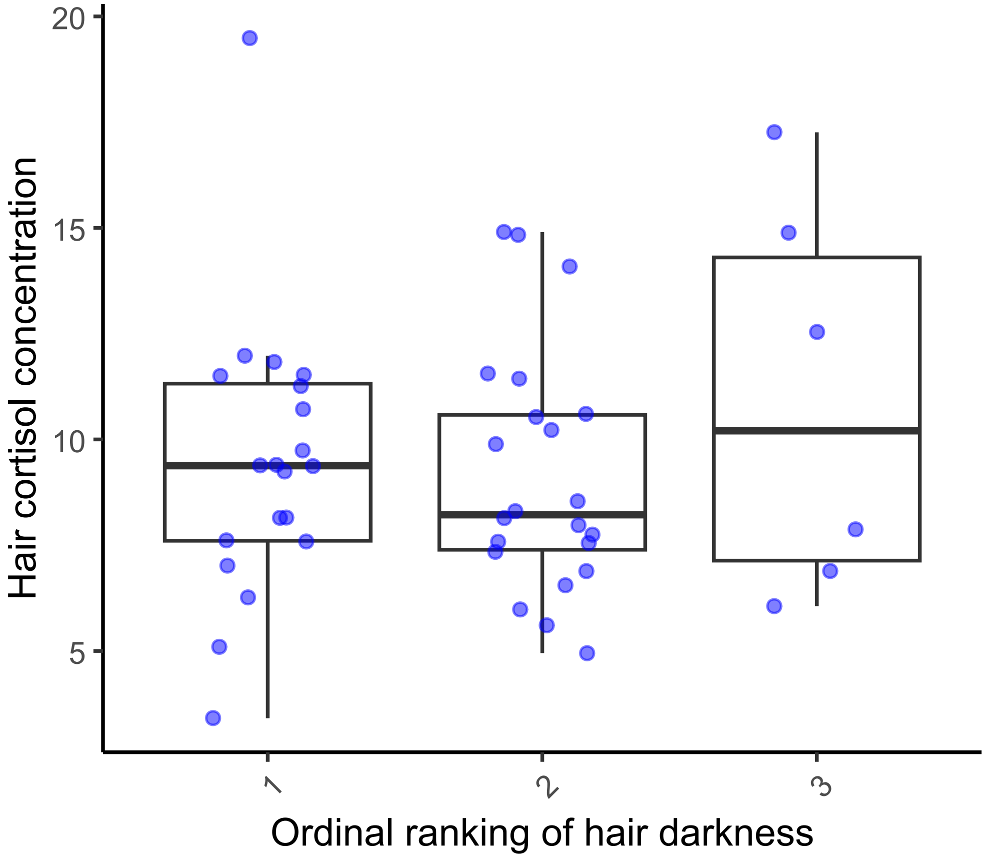

Figure **5-1**: Relationship between hair color and hair color concentration (*n* = 48). Hair color is scored on a three-point ordinal scale following Bennett and Hayssen (2010).

Relationship between cortisol measures

To assess changes in salivary cortisol over the 30-minute period in the dog park, we conducted a Pearson's product-moment correlation test of the log-transformed salivary cortisol values before and after time in the park. These values were significantly correlated ($r = 0.510$, $n = 48$, $p = 0.0002$, Figure 5-2). However, a paired t-test of the log-transformed salivary cortisol values did not detect a significant change in salivary cortisol after time spent in the dog park ($t = -1.492$, $n = 48$, $p = 0.1425$).

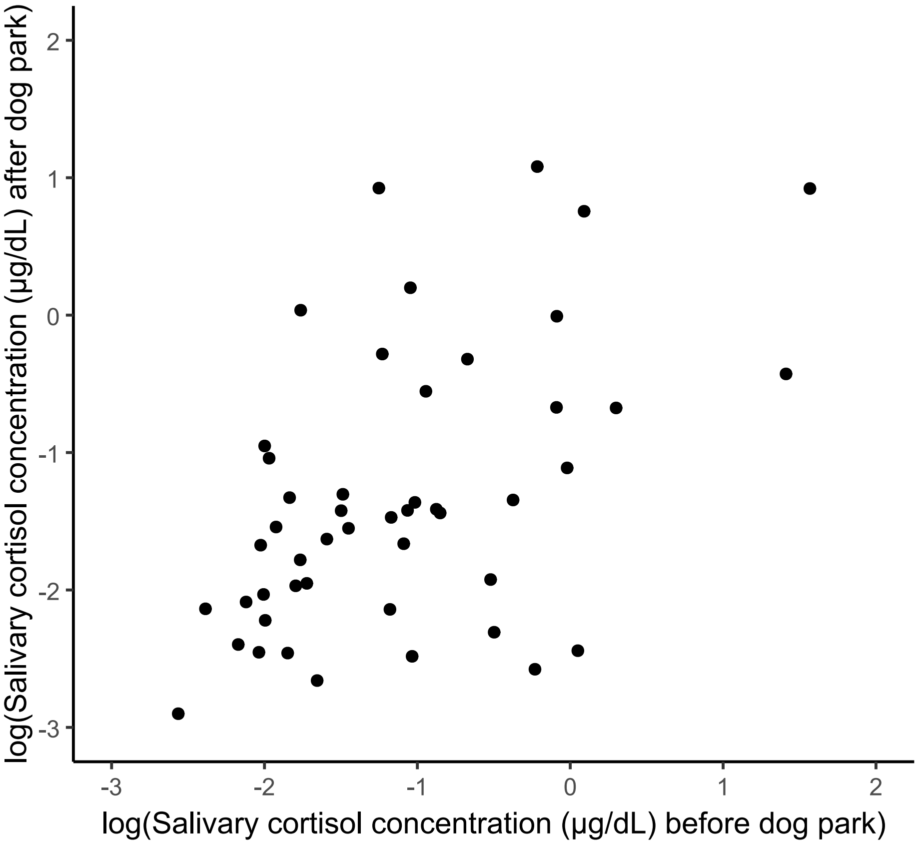

Figure **5-2**: Relationship between baseline salivary cortisol with salivary cortisol after 30 minutes in the dog park ($n = 48$). Cortisol concentrations are log-transformed.

To examine the relationship between salivary and hair cortisol, we tested whether hair cortisol concentration correlated with the log-transformed baseline salivary cortisol concentration (i.e., before the dogs entered the dog park), as this measure would be expected to best reflect the dog's typical cortisol levels. However, no significant correlation was found (Pearson's product-moment correlation test, r = -0.0298, n = 34, p = 0.867, Figure 5-3). When salivary cortisol was considered categorically, using a 0.4 μg/dL cutoff to categorize stress and grouping individuals into four categories based on whether they started and/or ended in the stressed range, no significant differences in hair cortisol concentrations were detected across categories (ANOVA, F = 1.526, n = 34, p = 0.228).

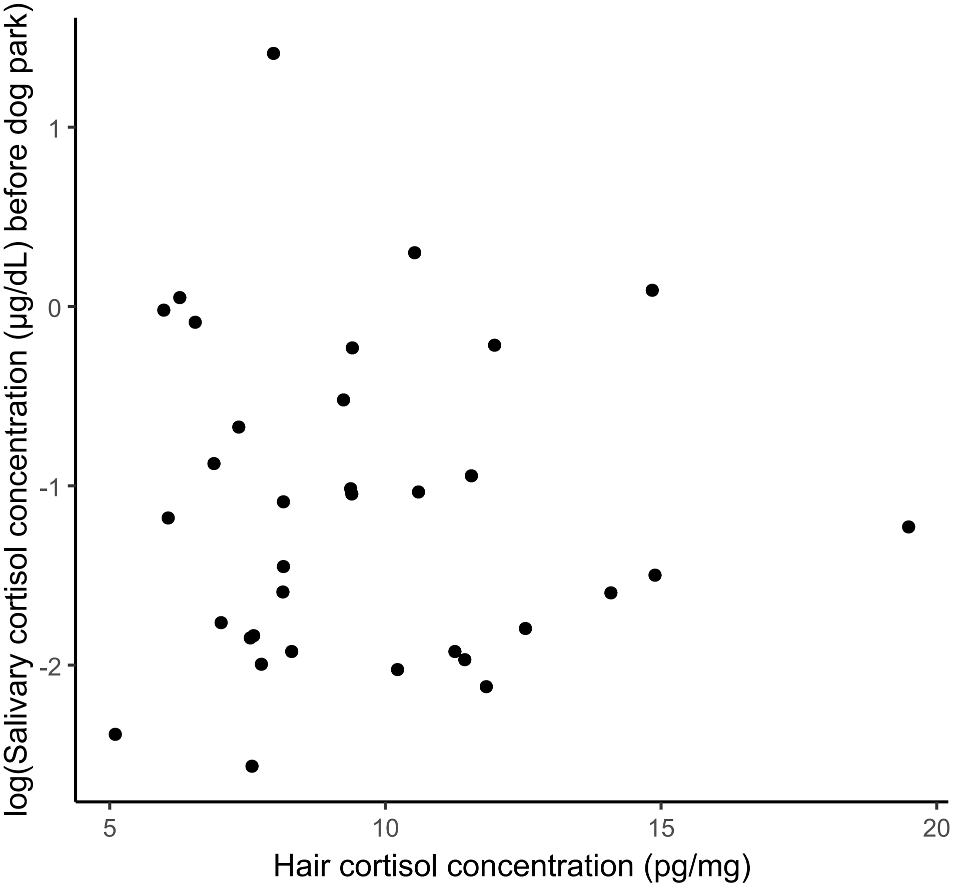

Figure **5-3**: Relationship between baseline log-transformed salivary cortisol with hair cortisol concentrations (n = 34).

Salivary cortisol compared to behavioral measures

To assess the relationship between fluctuations in salivary cortisol and behavioral measures of stress, we performed linear models to predict log-transformed salivary cortisol concentrations after 30 minutes in the dog park. The predictors included the baseline log-transformed salivary cortisol concentration and the behavioral measures of stress. Additionally, we performed ANOVA tests to compare behavioral stress measures across the four salivary cortisol categories based on whether the dog's cortisol level was above or below the 0.4 µg/dL cutoff before and after their time in the dog park.

The C-BARQ dimension of fear and anxiety was not a significant predictor of final log-transformed salivary cortisol after controlling for baseline levels ($\beta = 0.045$, $n = 26$, $p = 0.883$). C-BARQ fear and anxiety ratings also did not differ between stress categories (ANOVA, $F = 0.284$, $n = 28$, $p = 0.836$). The MCPQ-R dimension of neuroticism was not a significant predictor of final log-transformed salivary cortisol after controlling for baseline ($\beta = 0.003$, $n = 48$, $p = 0.729$), nor did it differ between stress categories (ANOVA, $F = 0.495$, $n = 50$, $p = 0.688$). The observed counts of stress behaviors during the behavioral observation did not significantly predict final log-transformed salivary cortisol after controlling for baseline ($\beta = 0.025$, $n = 47$, $p = 0.737$). However, a generalized linear model with a Poisson link function to predict counts of stress behavior using stress change categories found that dogs that started and ended as stressed had higher frequency of stress behaviors than the baseline of dogs that started and ended as unstressed ($\beta = 1.099$, $n = 49$, $p = 0.0001$, Figure 5-4). Whether or not dogs ate the treat following the umbrella task was not a significant predictor of final log-transformed salivary cortisol after controlling for baseline ($\beta = 0.184$, $n = 27$, $p = 0.647$).

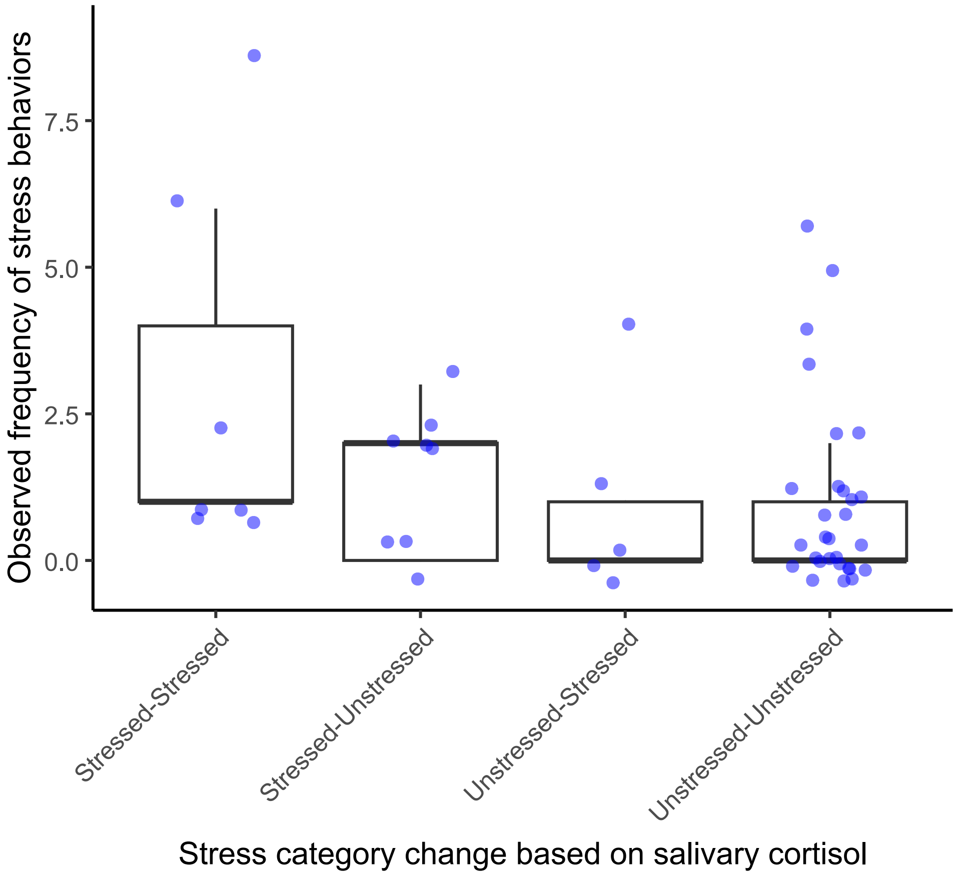

Figure **5-4**: Relationship between the change in salivary cortisol before and after time in dog park to the observed frequency of stress behaviors in dog park (*n* = 49). Categorical definitions of salivary cortisol define stressed as cortisol concentrations above 0.4 µg/dL and unstressed as concentrations below that threshold.

Hair cortisol compared to behavioral measures

We also examined how longer-term levels of cortisol, measured using hair cortisol concentrations, were related to the same behavioral measures of stress described above. Hair cortisol concentrations were not significantly associated with the C-BARQ fear and anxiety score (Pearson's product-moment correlation test, $r = 0.258$, $n = 31$, $p = 0.161$), nor was it associated with the MCPQ-R neuroticism score (Pearson's product-moment correlation test, $r = 0.073$, $n = 48$, $p = 0.621$). In a binomial generalized linear model, hair cortisol concentrations were not significantly associated with whether dogs ate the food in the umbrella task ($\beta = 0.029$, $n = 39$, $p = 0.774$). A generalized linear model with a Poisson link function to predict counts of stress behavior in the dog park did not find hair cortisol concentration to be a significant predictor ($\beta = 0.043$, $n = 45$, $p = 0.229$).

Power analyses

To better contextualize the results, we also performed power analyses to estimate the effect sizes we would reasonably be able to detect. Statistical power is the probability of attaining a statistically significant result given a particular population effect size and a particular sample size (Quach et al., 2022). Ideally, power analyses are conducted prior to the beginning of data collection so that researchers can make informed decisions about the sample size required for a particular effect size to be detected (Quach et al., 2022). Post hoc power analyses (those conducted after data is collected and analyzed) are widely used to contextualize null results, but this practice has come under criticism (Quach et al., 2022; Zhang et al., 2019). While post hoc power analyses often use the sample size effect size detected in a study in the place of the population effect size, simulations indicate that this usually results in highly biased power estimates (Quach et al., 2022; Zhang et al., 2019). Even though this power analysis was conducted post hoc, we tried to avoid the pitfalls of post hoc power analyses by conducting them as if they were prospective, rather than taking the effect sizes from our findings above. This can help contextualize the results without making the mistake of assuming the sample effect size is equivalent to the population one. For instance, we failed to find a relationship of hair color to hair cortisol concentrations despite this relationship being reported in the literature (Bennett & Hayssen, 2010). We simulated an ordinal variable with three levels and associated it with a normally distributed continuous outcome at various effect sizes and tested the rate of effects detected at various sample sizes (Figure 5-5). With the sample size of 48 that we used to test the relationship between hair cortisol concentration and hair color, we estimate around a 75% chance of detecting a correlation of 0.5 and around a 95% chance of detecting a correlation of 0.7. We also simulated the relationship between two normally distributed variables being compared with a correlation test (Figure 5-6). For our test of the relationship between salivary and hair cortisol, with a sample size of 34, we estimate an 85% chance of detecting a correlation of 0.5.

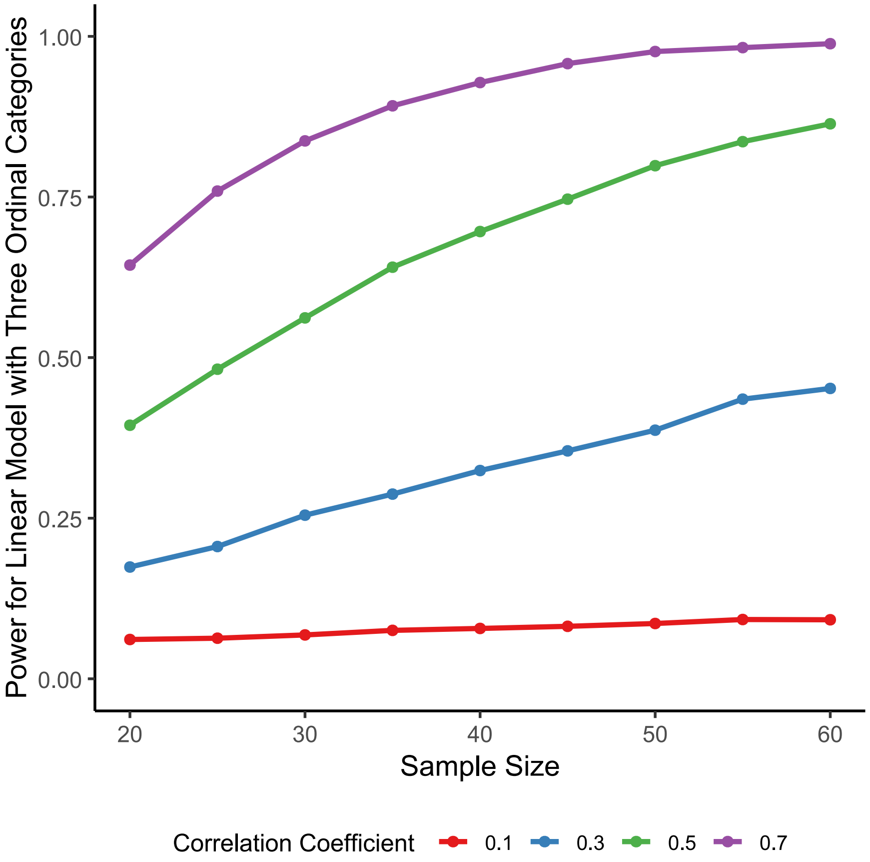

Figure **5-5**: Power analysis for detecting the relationship of a normally distributed response variable to an ordinal predictor with three levels.

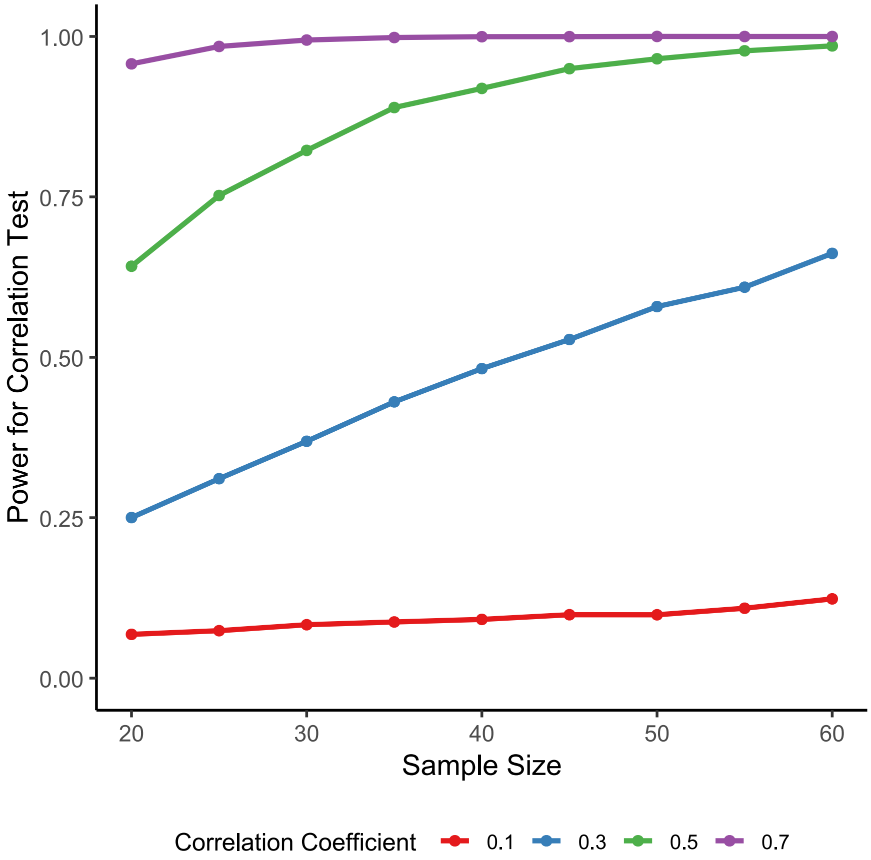

Figure **5-6**: Power analysis for detecting the relationship of a normally distributed response variable to a normally distributed predictor variable.

Discussion

These results, in combination with other recently published work, contextualize the reliability and validity of salivary cortisol as a measure of the biologically salient effects of cortisol in the body. The extremely strong (r = 0.9997) correlation of the duplicate assays indicates that the ELISA as a measure of salivary cortisol in a particular sample was reliable, in the methodological sense meaning that it can consistently produce the same values when measured multiple times (Martin & Bateson, 2017). The moderately strong correlation (r = 0.510) of salivary cortisol before and after time in the dog park shows some degree of reliability in salivary cortisol as a measure of different samples from the same dog, and it suggests that salivary cortisol levels across 30 minutes are stable enough to be correlated while also fluctuating enough to detect changes. The initial studies that validated the relationship between dog salivary cortisol and serum cortisol consisted of very small samples of laboratory housed adult dogs, usually of medium size (Beerda et al., 1996; Giannetto et al., 2014; Vincent & Michell, 1992). Recently, an attempt to validate salivary cortisol as a measure of serum cortisol in pet dogs of various breeds and in retriever puppies being trained as assistance dogs found no correlation between the two measures of cortisol in either sample (Ferrans et al., 2025). Combining the findings from this study with those of Ferrans et al., it seems that ELISAs can measure salivary cortisol (i.e., produce consistent measurements), but that salivary cortisol might not be a valid correlate of serum cortisol levels when applied to a heterogenous population of pet dogs. Serum cortisol is expected to be a more valid measure of HPA axis activity and physiological stress responses than salivary cortisol, as it directly causes physiological effects, and saliva concentrations are a byproduct of this (O'Connor et al., 2021).

Various factors can affect dogs' cortisol levels in ways that can confound relationships and make it difficult to interpret results. Demographic characteristics of the population can have some effects. For instance, intact females have been found to have higher cortisol levels than spayed females or than either intact or neutered males (Cobb et al., 2016). As this study only had three intact females, this is difficult to control for with this sample size, and although it is not likely to have a large effect on the results, it could add noise and make it harder to detect effects. Similarly, age can have a possible effect, with cortisol levels lower in dogs under 6 months old (Cobb et al., 2016). As before, such dogs make up a small proportion of this sample (five dogs at or under 6 months), so it is difficult to control for the effect of this, but it could be adding variability that makes interpretation difficult. A meta-analysis of dog salivary cortisol did not find an effect of dog weight or breed; however, even in this large meta-analysis, it was difficult to ascertain the effect of breed, as only a few breeds had a large enough sample to be able to accurately estimate the effect of breed (Cobb et al., 2016). This becomes all the more challenging to control for in studies such as this, where the sample consists of a heterogeneous sample of dogs of many breeds and mixes, with most breeds not having more than one or two individuals in the sample.

Besides demographic characteristics, there are various sampling-related variables that can affect cortisol and could have influenced our results. Cortisol follows a circadian rhythm (Giannetto et al., 2014), and while our observations were generally conducted during the same late-afternoon window, the extent of circadian variation in cortisol levels between dogs remains poorly understood. Salivary cortisol levels are higher on average when dogs are sampled in experimental settings such as laboratories as opposed to at home, as well as higher when dogs are away from their owners during the sampling (Cobb et al., 2016). The former of these considerations represents a substantial challenge for interpretation of the salivary cortisol results in this study as well as in other studies of dogs. Although the baseline salivary cortisol samples were collected several minutes after participants' arrival at the dog park, dogs had most likely had at least 10-15 minutes of time in transit on their way to the dog park. This is enough time for cortisol to increase relative to the baseline. The already elevated cortisol levels for the baseline measurements could be one reason why, on average, salivary cortisol had almost no change over the course of the observation. We would suggest that future studies incorporate sampling by the owners at home to get a more representative baseline of a dog's salivary cortisol. Although the owners were all present during the sampling, the salivary cortisol sampling was mostly done by an experimenter, but in a few cases, the owner sampled the cortisol when the dog was resistant to the experimenter doing so. While the effect of an owner versus stranger sampling the saliva is unknown, it is possible that this could have affected dogs' cortisol levels.

We also found no correlation between hair cortisol and salivary cortisol concentrations. However, previous work with a sample of 42 pet dogs found a very significant, moderately strong correlation ($r = 0.48$) between hair cortisol and salivary cortisol (Bennett & Hayssen, 2010). Based on our power analysis, we would expect an 85% chance of detecting an effect of that magnitude if it existed, so the inability to replicate this finding is surprising and suggests that the difference is more likely to be due to slightly different conditions between the studies changing the relationship, rather than simply a lack of power in this study. Bennett and Hayssen collected their saliva samples in the dogs' homes (Bennett & Hayssen, 2010), whereas in our study, we collected baseline samples at the dog park. This difference in sample collection sites might have affected the accuracy of our baseline measurements, as dogs may have already been experiencing heightened arousal due to the journey to the park or the proximity to it.

Overall, the results of this study do not provide strong evidence linking salivary cortisol to dogs' general tendencies towards stress as assessed through surveys and cognitive tasks. We found weak evidence suggesting a relationship between salivary cortisol and observed stress behaviors in the dog park, but only when a cut-off value (0.4 µg/dL) was applied. Several other recent studies have similarly failed to correlate dog salivary cortisol to observed responses to stressful stimuli (Ferrans et al., 2025; Hughes-Duvall, 2024), but one that did find a significant effect also used the same cut-off method (McPeake et al., 2021). When these findings are considered in tandem, we conclude that salivary cortisol might be a useful measure of short-term stress when levels exceed 0.4 µg/dL, but variations below that threshold appear to be too variable to provide reliable information.

Hair cortisol was not found to be significantly associated with any behavioral measures of short- or long-term stress in this study. Based on our power analysis, our sample size likely would have been sufficient to find correlations around 0.5 but insufficient for weaker relationships. Several other studies of dog hair cortisol have found that dark hair has lower cortisol concentrations than light hair (Bennett & Hayssen, 2010; Bowland et al., 2020), but we did not find a significant association of hair color with hair cortisol. In a population of dogs living in an Indigenous community in Nicaragua, many of which were used for hunting and which were often undernourished, hair cortisol was significantly negatively associated with overall body condition score, indicating that it can measure severe stress (Bowland et al., 2020). However, the stress measures used in this study, particularly owner ratings of fearfulness, may capture a narrower range of chronic stress compared to the Nicaraguan dogs. Additionally, more acute stress measures, such as stress behaviors observed in the dog park and salivary cortisol levels, were not associated with hair cortisol in our study.

In addition to the factors mentioned above, it is possible that the behavioral measurement tools used in this study (surveys, ethograms, umbrella task) may not accurately capture dogs' general tendency toward stress, or they may be assessing specific aspects of the stress response that have little correlation with cortisol. The effect sizes of these relationships could also be too small to detect at this sample size, especially when linking short- and long-term stress measures. The relationship between acute and chronic stress is complex, and it may involve a wide variety of stressors, each varying in frequency and severity, which contribute to chronic stress. Moreover, the body may recalibrate to a higher level of stress, potentially leading to a decrease in cortisol levels over time (O'Connor et al., 2021).

This study, along with several other recent studies, suggests future directions for measuring stress physiologically in dogs. While salivary cortisol is often used as a measure of the stress response, it is likely a weaker indicator than serum cortisol, which may be the preferred measure when it can be collected effectively (Ferrans et al., 2025). However, salivary cortisol is more commonly used because serum cortisol collection is often impractical and distressing for dogs, making saliva-based measures more desirable. Given these findings, it may be helpful to consider using cut-off values for salivary cortisol (e.g., 0.4 µg/dL) to indicate significantly elevated cortisol levels, rather than assuming that low-level variation in salivary cortisol reflects subtle stress responses in dogs (McPeake et al., 2021). Future research should focus on identifying the factors that confound salivary and hair cortisol measures and determining how to control for these variables effectively, which could help enhance the reliability of these biomarkers (Cobb et al., 2016). In addition, alternative biomarkers of stress should be explored. For example, one recent study found that while salivary cortisol did not change in response to a Strange Situation Task, salivary α-amylase levels did (Hughes-Duvall, 2024). Oxytocin, which is released during various social activities between individuals, has often been characterized as a social bonding hormone (Roney, 2016), and it is released during dog-human eye contact in both species (Nagasawa et al., 2009, 2015). However, oxytocin has many other functions throughout the body that seem to counteract the functions of the stress response, so it may be more accurate to think of oxytocin as coordinating an anti-stress response rather than simply serving a role of facilitating social bonds (Roney, 2016). In light of this, oxytocin could potentially be used as an indicator of stress reduction during positive interactions, warranting further exploration of how it might inversely correlate with stress.

Future research that improves our ability to quantify stress in dogs will have several applications. Changes to the stress response are believed to be a critical component of animal domestication (Sánchez-Villagra et al., 2016; Zeder, 2012), and experimental domestication of foxes causes changes to the HPA axis (Trut et al., 2009). However, as noted in Chapter 2, future research should attempt to quantify changes in the stress response between various pairs of domesticated and wild relatives, such as dogs and wolves, in order to better understand how humans have shaped other species' evolution. An improved ability to quantify stress also has clear applications for our understanding of how stress affects health. Chronic stress is linked to negative health outcomes in humans (O'Connor et al., 2021) and dogs (Dreschel, 2010), but the links between acute and chronic stress are poorly understood (Rohleder, 2019). The fact that dogs live alongside humans in a wide range of contexts makes them particularly well-suited to serve as a model for the effects of chronic stress on human health (Chapter 2).

References

Beerda, B., Schilder, M. B. H., Janssen, N. S. C. R. M., & Mol, J. A. (1996). The use of saliva cortisol, urinary cortisol, and cateoholamine measurements for a noninvasive assessment of stress responses in dogs. *Hormones and Behavior*, *30*(3), 272–279. https://doi.org/10.1006/hbeh.1996.0033

Bennett, A., & Hayssen, V. (2010). Measuring cortisol in hair and saliva from dogs: Coat color and pigment differences. *Domestic Animal Endocrinology*, *39*(3), 171–180. https://doi.org/10.1016/j.domaniend.2010.04.003

Blodgett, J., Walter, D., MacKenzie, J. A., Gump, B. B., & Bendinskas, K. (2017). Both hair cortisol and perceived stress during fall exams decrease after the winter break. *Austin Biochemistry*, *2*(1), 1007–1011. http://austinpublishinggroup.com/biochemistry/download.php?file=fulltext/biochemistry-v2-id1007.pdf

Boonstra, R. (2013). Reality as the leading cause of stress: rethinking the impact of chronic stress in nature. *Functional Ecology*, *27*(1), 11–23. https://doi.org/10.1111/1365-2435.12008

Bowland, G. B., Bernstein, R. M., Koster, J., Fiorello, C., Brenn-White, M., Liu, J., Schwartz, L., Campbell, A., von Stade, D., Beagley, J., Pomerantz, J., González, A., Quick, M., McKinnon, K., Aghaian, A., Sparks, C., & Gross, J. B. (2020). Fur color and nutritional status predict hair cortisol concentrations of dogs in Nicaragua. *Frontiers in Veterinary Science*, *7*(October), 1–10. https://doi.org/10.3389/fvets.2020.565346

Bray, E. E., Gruen, M. E., Gnanadesikan, G. E., Horschler, D. J., Levy, K. M., Kennedy, B. S., Hare, B. A., & MacLean, E. L. (2020). Cognitive characteristics of 8-to-10-week-old assistance dog puppies. *Animal Behaviour*, *166*, 193–206. https://doi.org/10.1016/j.anbehav.2020.05.019

Cagan, A., & Blass, T. (2016). Identification of genomic variants putatively targeted by selection during dog domestication. *BMC Evolutionary Biology*, *16*(1), 1–13. https://doi.org/10.1186/s12862-015-0579-7

Cobb, M. L., Iskandarani, K., Chinchilli, V. M., & Dreschel, N. A. (2016). A systematic review and meta-analysis of salivary cortisol measurement in domestic canines. *Domestic Animal Endocrinology*, *57*, 31–42. https://doi.org/10.1016/j.domaniend.2016.04.003

Dreschel, N. A. (2010). The effects of fear and anxiety on health and lifespan in pet dogs. *Applied Animal Behaviour Science*, *125*(3–4), 157–162. https://doi.org/10.1016/j.applanim.2010.04.003

Ferrans, M., Salomons, H., Moore, K., White, P., Hare, B., & Gruen, M. E. (2025). Salivary cortisol is an unreliable correlate of serum cortisol in adult pet dogs and assistance dog puppies. *Scientific Reports*, *15*(1), 1–11.

Friard, O., & Gamba, M. (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution*, *7*(11), 1325–1330. https://doi.org/10.1111/2041-210X.12584

Giannetto, C., Fazio, F., Assenza, A., Alberghina, D., Panzera, M., & Piccione, G. (2014). Parallelism of circadian rhythmicity of salivary and serum cortisol concentration in normal dogs. *Journal of Applied Biomedicine*, *12*(4), 229–233. https://doi.org/10.1016/j.jab.2014.01.009

Hughes-Duvall, K. (2024). *Does early life history influence a novel biomarker for stress in dogs and predict their attachment to their owners?*

Lamon, T. K., Slater, M. R., Moberly, H. K., & Budke, C. M. (2021). Welfare and quality of life assessments for shelter dogs: A scoping review. *Applied Animal Behaviour Science*, *244*(September), 105490. https://doi.org/10.1016/j.applanim.2021.105490

Ley, J. M., Bennett, P. C., & Coleman, G. J. (2008). A refinement and validation of the Monash Canine Personality Questionnaire (MCPQ). *Applied Animal Behaviour Science*, *116*, 220–227. https://doi.org/10.1016/j.applanim.2008.09.009

Martin, P., & Bateson, P. (2017). *Measuring behaviour: an introductory guide* (3rd ed.). Cambridge University Press.

McPeake, K. J., Collins, L. M., Zulch, H., & Mills, D. S. (2021). Behavioural and physiological correlates of the Canine Frustration Questionnaire. *Animals*, *11*(3346), 1–15.

Miller, G. E., Cohen, S., & Ritchey, A. K. (2002). Chronic psychological stress and the regulation of pro-inflammatory cytokines: A glucocorticoid-resistance model. *Health Psychology*, *21*(6), 531–541. https://doi.org/10.1037/0278-6133.21.6.531

Nagasawa, M., Kikusui, T., Onaka, T., & Ohta, M. (2009). Dog's gaze at its owner increases owner's urinary oxytocin during social interaction. *Hormones and Behavior*, *55*(3), 434–441. https://doi.org/10.1016/j.yhbeh.2008.12.002

Nagasawa, M., Mitsui, S., En, S., Ohtani, N., Ohta, M., Sakuma, Y., Onaka, T., Mogi, K., & Kikusui, T. (2015). Oxytocin-gaze positive loop and the coevolution of human-dog bonds. *Science*, *348*(6232), 333–336.

O'Connor, D. B., Thayer, J. F., & Vedhara, K. (2021). Stress and health: a review of psychobiological processes. *Annual Review of Psychology*, *72*, 663–688. https://doi.org/10.1146/annurev-psych-062520-122331

Ottenheimer Carrier, L., Cyr, A., Anderson, R. E., & Walsh, C. J. (2013). Exploring the dog park: Relationships between social behaviours, personality and cortisol in companion dogs. *Applied Animal Behaviour Science*, *146*(1–4), 96–106. https://doi.org/10.1016/j.applanim.2013.04.002

Protopopova, A. (2016). Effects of sheltering on physiology, immune function, behavior, and the welfare of dogs. *Physiology and Behavior*, *159*, 95–103. https://doi.org/10.1016/j.physbeh.2016.03.020

Quach, N. E., Yang, K., Chen, R., Tu, J., Xu, M., Tu, X. M., & Zhang, X. (2022). Post-hoc power analysis: a conceptually valid approach for power based on observed study data. *General Psychiatry*, *35*(4), 1–7. https://doi.org/10.1136/gpsych-2022-100764

R Core Team. (2023). *R: a language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.r-project.org

Raul, J. S., Cirimele, V., Ludes, B., & Kintz, P. (2004). Detection of physiological concentrations of cortisol and cortisone in human hair. *Clinical Biochemistry*, *37*(12), 1105–1111. https://doi.org/10.1016/j.clinbiochem.2004.02.010

Rohleder, N. (2019). Stress and inflammation – The need to address the gap in the transition between acute and chronic stress effects. *Psychoneuroendocrinology*, *105*(August 2018), 164–171. https://doi.org/10.1016/j.psyneuen.2019.02.021

Roney, J. R. (2016). Theoretical frameworks for human behavioral endocrinology. *Hormones and Behavior*, *84*, 97–110. https://doi.org/10.1016/j.yhbeh.2016.06.004

Salomons, H., Smith, K. C. M., Callahan-Beckel, M., Callahan, M., Levy, K., Kennedy, B. S., Bray, E. E., Gnanadesikan, G. E., Horschler, D. J., Gruen, M., Tan, J., White, P., VonHoldt, B. M., MacLean, E. L., & Hare, B. (2021). Cooperative communication with humans evolved to emerge early in domestic dogs. *Current Biology*, *31*(July), 1–8. https://doi.org/10.1016/j.cub.2021.06.051

Sánchez-Villagra, M. R., Geiger, M., & Schneider, R. A. (2016). The taming of the neural crest: A developmental perspective on the origins of morphological covariation in domesticated mammals. *Royal Society Open Science*, *3*(6). https://doi.org/10.1098/rsos.160107

Sapolsky, R. M. (2004). Social status and health in humans and other animals. *Annual Review of Anthropology*, *33*(1), 393–418. https://doi.org/10.1146/annurev.anthro.33.070203.144000

Snyder-Mackler, N., Burger, J. R., Gaydosh, L., Belsky, D. W., Noppert, G. A., Campos, F. A., Bartolomucci, A., Yang, Y. C., Aiello, A. E., O'Rand, A., Harris, K. M., Shively, C. A., Alberts,

S. C., & Tung, J. (2020). Social determinants of health and survival in humans and other animals. *Science*, *368*(6493), eaax9553. https://doi.org/10.1126/science.aax9553

Trut, L., Oskina, I., & Kharlamova, A. (2009). Animal evolution during domestication: the domesticated fox as a model. *Bioessays*, *31*(3), 349–360. https://doi.org/10.1038/jid.2014.371

Trut, L., Plyusnina, I. Z., & Oskina, I. N. (2004). An experiment on fox domestication and debatable issues of evolution of the dog. *Russian Journal of Genetics*, *40*(6), 644–655.

Vega Ocasio, D., Stewart-Ibarra, A. M., Sippy, R., Li, C., McCue, K., Bendinskas, K. G., Gump, B. B., Cueva-Aponte, C., Ayala, E. B., Morrell, C. N., & Dye, T. D. (2021). Social stressors, arboviral infection, and immune dysregulation in the coastal lowland Region of Ecuador: A mixed methods approach in ecological perspective. *American Journal of Tropical Medicine and Hygiene*, *105*(3), 756–765. https://doi.org/10.4269/ajtmh.20-1625

Vincent, I. C., & Michell, A. R. (1992). Comparison of cortisol concentrations in saliva and plasma of dogs. *Research in Veterinary Science*, *53*(3), 342–345. https://doi.org/10.1016/0034-5288(92)90137-Q

Wilkins, A. S., Wrangham, R. W., & Tecumseh Fitch, W. (2014). The “domestication syndrome” in mammals: A unified explanation based on neural crest cell behavior and genetics. *Genetics*, *197*(3), 795–808. https://doi.org/10.1534/genetics.114.165423

Wilkins, V., Evans, J., Park, C., Fitzpatrick, A. L., Creevy, K. E., & Ruple, A. (2024). Validation of the shortened version of the Canine Behavioral Assessment and Research Questionnaire (C-BARQ) using participants from the Dog Aging Project. *PLoS ONE*, *19*(4 April), 1–15. https://doi.org/10.1371/journal.pone.0299973

Zeder, M. A. (2012). The domestication of animals. *Journal of Anthropological Research*, *68*(2), 161–190.

Zhang, Y., Hedo, R., Rivera, A., Rull, R., Richardson, S., & Tu, X. M. (2019). Post hoc power analysis: is it an informative and meaningful analysis? *General Psychiatry*, *32*(4), 3–6. https://doi.org/10.1136/gpsych-2019-100069

Chapter 6

Microbial Correlates of Domestication and Stress Physiology in Domestic Dogs

Introduction

The microbiome is the diverse ecosystem of bacteria, protists, viruses, fungi, and other organisms that resides within the body of a multicellular organism (Hou et al., 2022). In humans, canines, and other mammals, the gastrointestinal tract (i.e., gut) and oral cavity harbor the largest, most diverse, and most functionally relevant microbial communities (Bäckhed et al., 2012; Kennedy & Chang, 2020; Pereira & Clemente, 2021). In addition to microbes that are parasitic or commensal, which are harmful or neutral to the host, many mammalian microbes have symbiotic relationships that benefit both the host and the microbe (Hou et al., 2022). Through diverse pathways, microbes support host health by facilitating food digestion and absorption, training and contributing to the functioning of the immune system, and producing health-promoting metabolites (e.g., bile acids, short-chain fatty acids, vitamins, lipids) (J. Liu et al., 2022; Valdes et al., 2018).

The microbiomes of domesticated animals, such as dogs, are particularly interesting to study both for understanding how domestication has altered these animals and for serving as models to investigate the human microbiome and its interactions with health and lifestyle factors. A comparison of the gut microbiomes of domesticated mammals with their wild relatives revealed a distinct microbial signature associated with domestication, and this signature was paralleled in a comparison of humans relative to chimpanzees (Reese et al., 2021). The same study performed a diet swap of dogs and wolves as well as domesticated and wild mice, and the gut microbiomes were found to partially, but not fully, converge (Reese et al., 2021). Similarly, another study swapping dogs' diets from kibble to raw meat found a convergence in their gut microbiomes to be more similar to those of wolves eating raw meat (J. Xu et al., 2021). In addition to dogs and wolves differing significantly in the composition of their gut microbiomes (Reese et al., 2021; J. Xu et al., 2021), they also differ in their oral microbiomes (Podar et al., 2024). Beyond interspecies comparisons, differences within dog populations are also of interest. For example, dogs living in rural villages have been found to have more diverse gut microbiomes than dogs living in industrialized contexts—a pattern that parallels findings in humans (Yarlagadda et al., 2022).

The relationship between diet and the microbiome is a particularly interesting area in which to compare dogs and humans. Just as human diets are highly variable around the world, dogs also consume a diverse range of foods depending on the society in which they live. Archaeological studies comparing the stable isotopes of dogs and humans have found that dogs can serve as an effective proxy for human diets across different societies (Guiry, 2012, 2013). Dogs have evolved genetic adaptations to the diets of the different societies they inhabit, such as increased copy number of amylase in dogs that consume more starches (Axelsson et al., 2013; Reiter et al., 2016), similar to the changes seen in humans who eat more starches (Perry et al., 2007), and selection on alleles that increase expression of the lactase gene in dogs in areas with high dairy consumption (Y. H. Liu et al., 2021), similar to the changes seen in many pastoralist and agriculturalist human populations (Ségurel & Bon, 2017). In addition to genetic changes, the microbiome represents another potential mechanism through which dogs may have adapted to new diets during both their initial domestication and their global spread. Ancient DNA sequenced from dog coprolites from Bronze Age Italy shows that these dogs had not yet evolved the high copy number of amylase genes seen in modern European dogs, but the alpha-amylase genes of the dogs' microbes were enriched well beyond the level seen in modern dogs (Rampelli et al., 2021). The microbiome may also help dogs adapt to a dairy-rich diet in addition to genetic mechanisms. A study of dogs from four countries found that those living in areas where dairy products such as yogurt are part of their diet harbor lactose-metabolizing bacteria like *Lactobacillus*, suggesting a microbial adaptation that parallels host dietary practices (Yarlagadda et al., 2022).

The importance of the microbiome to the domestication and local adaptation of dogs could extend beyond just diet. In recent decades, the microbiome, due to its numerous associations with a wide range of conditions, has been increasingly recognized as both a marker of overall health as well as a mechanistic pathway through which health and disease are influenced (Gancz & Weyrich, 2023; Hou et al., 2022). These associations are believed to arise due to the ability of microbes and their metabolites to translocate throughout the body, potentially contributing to disease risk (Martinez et al., 2017; Rahman et al., 2023), because chronic health conditions can alter the body in ways that disrupt microbial ecosystems (Madhogaria et al., 2022), or due to shared mediating factors, such as diet, that influence both microbial communities and disease outcome (Mansour et al., 2021; Ross et al., 2024). Since the microbiome affects the risk of various health conditions, factors affecting the microbiome could be selected for in dogs via the microbiome's effect on systemic health.

The genomic evidence of selection during dog domestication points to the importance of both diet and the stress response (Axelsson et al., 2013; Cagan & Blass, 2016). Comparisons of dogs and wolves show that reduced fear and increased social cognition in dogs are among the major differences (Salomons et al., 2021). The changes to dogs' stress response and social interactions with humans as a result of domestication are noteworthy given that chronic stress and social connectedness are linked to health outcomes. For instance, chronic stress is associated with shorter lifespans and increased incidence of chronic illness (O'Connor et al., 2021; Yegorov et al., 2020), while strong social relationships are linked to longer, healthier lives (Snyder-Mackler et al., 2020; Yang et al., 2016). In dogs as well, stress and social support are linked to health outcomes (Dreschel, 2010; McCoy et al., 2023). However, the mechanisms driving these associations are not fully understood. The links between the microbiome and systemic health suggest it may act as a mechanistic bridge between health outcomes and their potential social or environmental determinants. Because differences in microbial composition have been linked to both stress and social interaction (Archie & Tung, 2015; Dill-McFarland et al., 2019; Sarkar et al., 2024; Tofani et al., 2024; Wu et al., 2021), examining the microbiome may provide important insights into how these psychosocial factors influence health.

A growing body of research indicates that there is a bidirectional relationship between the microbiome and stress. This has especially been studied in the case of the gut microbiome. (Marwaha et al., 2025). The hypothalamic-pituitary-adrenal (HPA) axis causes a cascade of hormone releases that result in the release of the glucocorticoid hormone cortisol, which makes glucose available for the muscles while reducing bodily functions like digestion and the immune system which allows an organism to optimize its energy to respond to the stressor (O’Connor et al., 2021). Changes to digestion can affect the gut microbiome, such as slowing the fecal transit of the gastrointestinal tract and decreasing gastric acid secretion, both of which can shift the composition of the gut microbiome (Marwaha et al., 2025). Chronic activation of the HPA axis can however lead to the desensitization of glucocorticoid receptors and eventually lead to a state of chronic low-level inflammation, which is related to a variety of health problems (O’Connor et al., 2021). Inflammation can shift the composition of the microbiome, and while a healthy microbiome can help prevent inflammation, dysbiosis can change this and cause proinflammatory responses (Marwaha et al., 2025). Inflammatory cytokines can cause changes in gene regulation that affect the tight junctions of the digestive epithelium, which increases gut permeability, thereby letting microbes and their metabolites escape into the bloodstream, which can increase inflammation and cause health problems (Marwaha et al., 2025). Byproducts of the microbiome such as short-chain fatty acids (SCFAs) are important for brain activity and immune signaling, and stress in mouse models has caused changes to the gut microbiome that result in decreased

SCFAs (Marwaha et al., 2025). While the oral microbiome has received less attention, there have also been found to be feedback loops between periodontal disease and inflammation, and the translocation of oral microbes and their metabolites can also have health implications like those discussed above for the gut microbiome (Gancz & Weyrich, 2023). The associations between dogs' microbiome and stress are still being explored. The composition of the gut microbiome has been found to be associated with fear and aggression in dogs (Kirchoff et al., 2019; Mondo et al., 2020). Dogs and humans from the same household had significantly more shared microbes on their skin than with other individuals of the opposite species (Song et al., 2013), so the social interactions between dogs and humans may be important for shaping the microbiomes of each species.

Understanding the relationship between dogs' microbiomes and diet, stress, and social factors will not only help us understand dog domestication but also our own health. Dogs live among humans all over the world and have similar variation in diet, exercise, social interactions, antibiotic usage, and other environmental variables that are relevant to health. In the US, the rates, age trajectories, and comorbidities of broad causes of death are fairly similar between humans and dogs (Hoffman et al., 2018). This suggests that dogs can be a useful model for studying human health and aging (Hoffman et al., 2018; Ruple et al., 2022). The role of the microbiome in various health conditions can be explored by looking at dogs. For instance, noncommunicable diseases tend to rise in humans in association with industrialization (Wagner & Brath, 2012). Industrialization is linked to changes in the microbiome of humans (Jha et al., 2018; Mancabelli et al., 2017; Tian et al., 2025) and dogs (Yarlagadda et al., 2022). Further exploring the factors that affect the microbiome and the associations of the microbiome with systemic health will help elucidate the role of the microbiome in these patterns. Examining whether the patterns in dogs are similar to those in humans could help with determining the causal mechanisms.

In this study, we contribute to the characterization of the gut and oral microbiomes of dogs with the goal of investigating how these microbial communities are associated not only with domestication, but also with cognitive and physiological traits such as behavior and stress responses. In particular, this study involves comprehensive data collection on each dog, resulting in a rich metadata set that includes information on demographics, social behavior, and cortisol levels. This integrative approach enables us to examine whether variation in the microbiome is linked to individual differences in cognition, sociality, and physiological stress. We analyze associations between the composition of the gut and oral microbiomes and dogs' behavioral traits, cortisol concentrations, and demographic factors. In addition, we compare microbiomes from our sample with published datasets of dogs and wolves to better understand how domestication and environmental context may have shaped microbiome composition and whether those changes are connected to behavioral and physiological adaptations.

Methods

Data collection

A sample of dogs and their human owners was recruited from Tudek Dog Park in State College, Pennsylvania, United States. This sample represents companion dogs living in an industrialized context, specifically those that frequent off-leash dog parks. Microbiome samples were collected and sequenced from 46 dogs: gut microbiomes were sequenced for 15 dogs, and oral microbiomes for 43 dogs. The sample included an equal number of female and male dogs (*n* = 23 each), with 80% of individuals reported as spayed or neutered. The median age was 2 years, with ages ranging from just under 4 months to 9 years. The sample included a variety of purebred and mixed-breed dogs. One owner reported that their dog was currently receiving antibiotics, one was unsure, and the remaining owners indicated their dogs were not on antibiotics at the time of sampling.

Fecal samples were collected from the ground at the dog park during a 30-minute observation of each dog. Samples were gathered in plastic bags, and within 30 minutes, gloved hands and cotton swabs were used to open the feces and collect a small sample from the interior to minimize environmental contamination. The samples were then labeled, placed into small cryovials, stored on ice, and transported to a -20°C freezer for long-term storage.

At the second visit, the dogs' oral microbiomes were sampled in the laboratory. Salimetrics Children's Swabs were placed on the left buccal side of the dog's mouth and swabbed for at least 30 seconds. A treat was held in front of the dog to stimulate salivation but was not given until after the sample was collected. The swabs were then placed in storage tubes, labeled, and placed on ice. Finally, the samples were transported to a -20°C freezer for storage.

In addition to the collection of gut and oral microbiome samples, various other metadata were gathered. Owners completed surveys providing basic demographic information about the dogs, as well as the Monash Canine Personality Questionnaire-Revised (MCPQ-R) (Ley et al., 2008), which was used to assess the dogs' behavior. Salivary cortisol was sampled before and after a 30-minute observation session in the dog park, and hair cortisol was sampled in the laboratory during the second session. At this visit, dogs performed a battery of cognitive tasks, including a temperament task where an umbrella was opened suddenly in front of the dog and dropped in front of a treat, and the dog was given 30 seconds in which to have the chance to eat the treat (Bray et al., 2020).

In addition to the data collected from the Pennsylvania dogs described above, samples were compared to those from several published studies assessing dog and wolf gut and oral microbiomes. Reese et al. published gut microbiome samples (European Nucleotide Archive: PRJEB36262) from 16 dogs and 19 wolves from a Minnesota sanctuary (Reese et al., 2021). Xu et al. published gut microbiome samples (SRA Database: PRJNA729861) from 6 dogs and 6 wolves from a Chinese research center and zoo, respectively (J. Xu et al., 2021). In both studies, a diet swap was performed, so only the baseline samples were used for comparison in this study. Podar et al. published oral microbiome samples (GenBank SRA: PRJNA1040034) from 17 oral disease-free companion dogs and 15 wild Yellowstone National Park wolves (Podar et al., 2024).

Sample and data processing

Saliva samples were processed in a laboratory at the Pennsylvania State University, while fecal samples were shipped on dry ice to New York University-Abu Dhabi for processing. Saliva samples were thawed and centrifuged to separate the liquid saliva from the swab prior to DNA extraction. Fecal samples were transferred into a preservation buffer and held at room temperature for 7-10 days before DNA extraction, to match the conditions used in a comparative dataset of similarly buffered samples in a forthcoming publication (Jha, pers. comm.). DNA from oral microbiome samples was extracted using the DNeasy Powersoil Pro kit (QIAGEN #47014), with extraction blank controls included to monitor contamination. The composition of bacterial communities was characterized by amplifying the V3-V4 hypervariable region of the 16S rRNA gene using PCR using 16S_515F and 16S_808R_Variable primers. Amplified DNA was sent for sequencing. All steps for the gut microbiome samples were processed in a single batch, while the oral microbiome samples were processed in two separate batches. PCR negative controls were included for the second batch of oral microbiome samples. Extraction blank controls from the DNA extraction of the gut microbiome samples were also sequenced.

FASTQ files were used as inputs and imported into QIIME2 (version 2023.9.2) (Bolyen et al., 2019). The samples were demultiplexed using the demux plugin and quality-filtered using DADA2 (Callahan et al., 2016). For the oral microbiome samples, sequences were trimmed to

249 bases for forward reads and 240 bases for reverse reads to maintain quality scores exceeding 20. For gut microbiome samples, sequences were trimmed to 226 bases (forward) and 223 bases (reverse). Singleton features were removed the dataset. To identify potential contaminants, the decontam package (Davis et al., 2018) was run separately for each sequencing batch, using a prevalence threshold of 0.5. Feature tables were then constructed, and taxonomic classification was performed in QIIME2 using the Silva 138 99% Native Bayes Classifier (Quast et al., 2013).

Data analysis

To better understand the factors associated with variation in the microbiome, several statistical and ecological analyses were implemented. Aitchison beta diversity was calculated using the Gemelli plugin (Martino et al., 2021) in QIIME 2. Associations with variables of interest were tested using the Adonis package (Oksanen et al., 2018) to run a PERMANOVA test, a non-parametric, permutational multivariate model well-suited for ecological distance matrices (McArdle & Anderson, 2001). Differential abundance analysis was performed using MaAsLin2 (Mallick et al., 2021) in R statistical software version 4.5.0 (R Core Team, 2023). For this, the prevalence data was filtered to those features prevalent in at least 10% of samples and with a mean abundance of at least 5%, the data were normalized, and a Benjamini-Hochberg FDR correction was applied for multiple comparisons (Benjamini & Hochberg, 1995). Shannon diversity was used as the alpha diversity metric, with differences assessed using Kruskal–Wallis tests for categorical variables and Spearman correlation for continuous variables. Microbiome analyses for the collected samples were conducted at the ASV level. For comparisons with previously published datasets, analyses were performed at the genus level to minimize methodological variation across studies.

Results

Oral microbiome

Oral microbiome samples were successfully sequenced from 43 dogs. The most prevalent bacterial genera identified across samples included *Frederiksenia*, *Porphyromonas*, an unidentified genus within the *Pasteurellaceae* family, *Moraxella*, and an unclassified genus within the *Neisseriaceae* family (Figure 6-1).

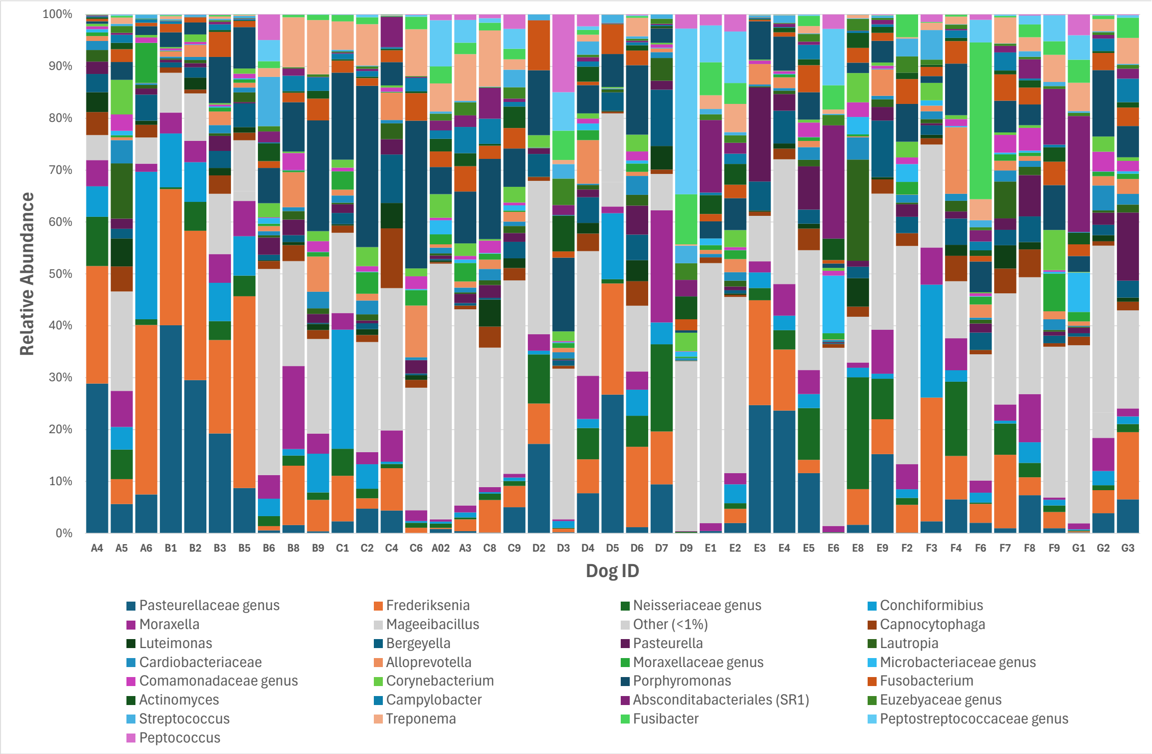

Figure **6-1**: Taxonomic bar plot showing the relative abundance of bacterial genera detected via 16S rRNA sequencing in oral microbiome samples from dogs (*n* = 43). Each bar represents an individual dog, labeled by Dog ID on the x-axis. Genera comprising less than 1% of the total abundance across all samples are grouped under the category “Other taxa.”

The oral microbiome samples were sequenced in two batches of 14 and 29 samples. A PERMANOVA test indicated a significant difference in beta diversity between sequencing batches ($F = 5.007$, $n = 43$, $p = 0.008$), so sequencing batch was included as a covariate in subsequent analyses. After controlling for batch effects, no significant difference in oral microbiome beta diversity was observed between the sexes (PERMANOVA, $F = 0.074$, $n = 43$, $p = 0.956$). However, dogs that were spayed or neutered had significantly different oral microbiome beta diversity than unfixed dogs (PERMANOVA, $F = 13.495$, $n = 43$, $p = 0.002$, Figure 6-2). Oral microbiome beta diversity also varied across dogs as a function of age (PERMANOVA, $F = 12.178$, $n = 43$, $p = 0.001$, Figure 6-3). Notably, age and neuter status were not independent, as intact dogs were significantly younger than spayed or neutered dogs (t = 4.010, $p = 3.37 \times 10^{-4}$). However, when age, neuter status, and sequencing batch were all included in the same PERMANOVA model, each had a significant effect (age: $F = 7.941$, $p = 0.003$; neuter status: $F = 9.022$, $p = 0.002$; sequencing batch: $F = 6.835$, $p = 0.003$).

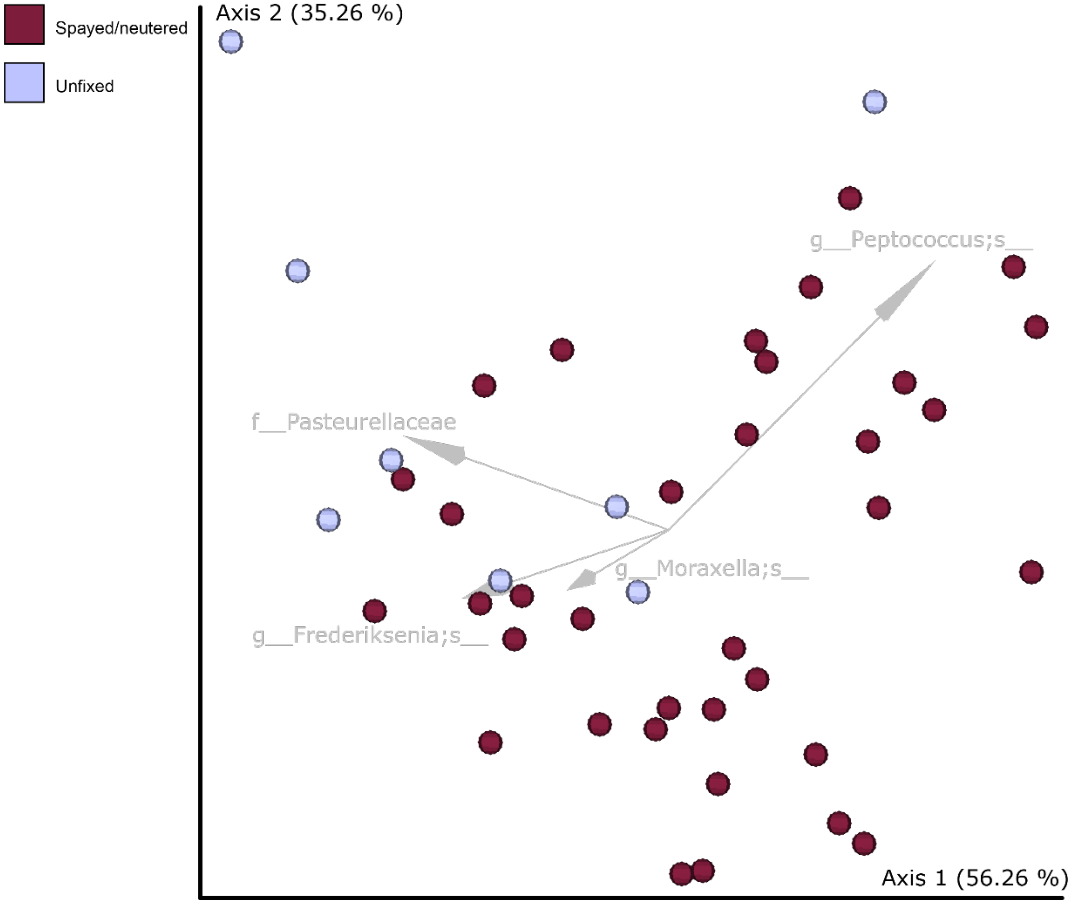

Figure **6-2**: Principal Coordinates Analysis (PCoA) biplot showing the first two axes of Aitchison beta diversity among oral microbiome samples from dogs ($n = 43$) in relation to spay/neuter status. Each point represents an individual dog, with proximity on the plot indicating greater similarity in microbial composition.

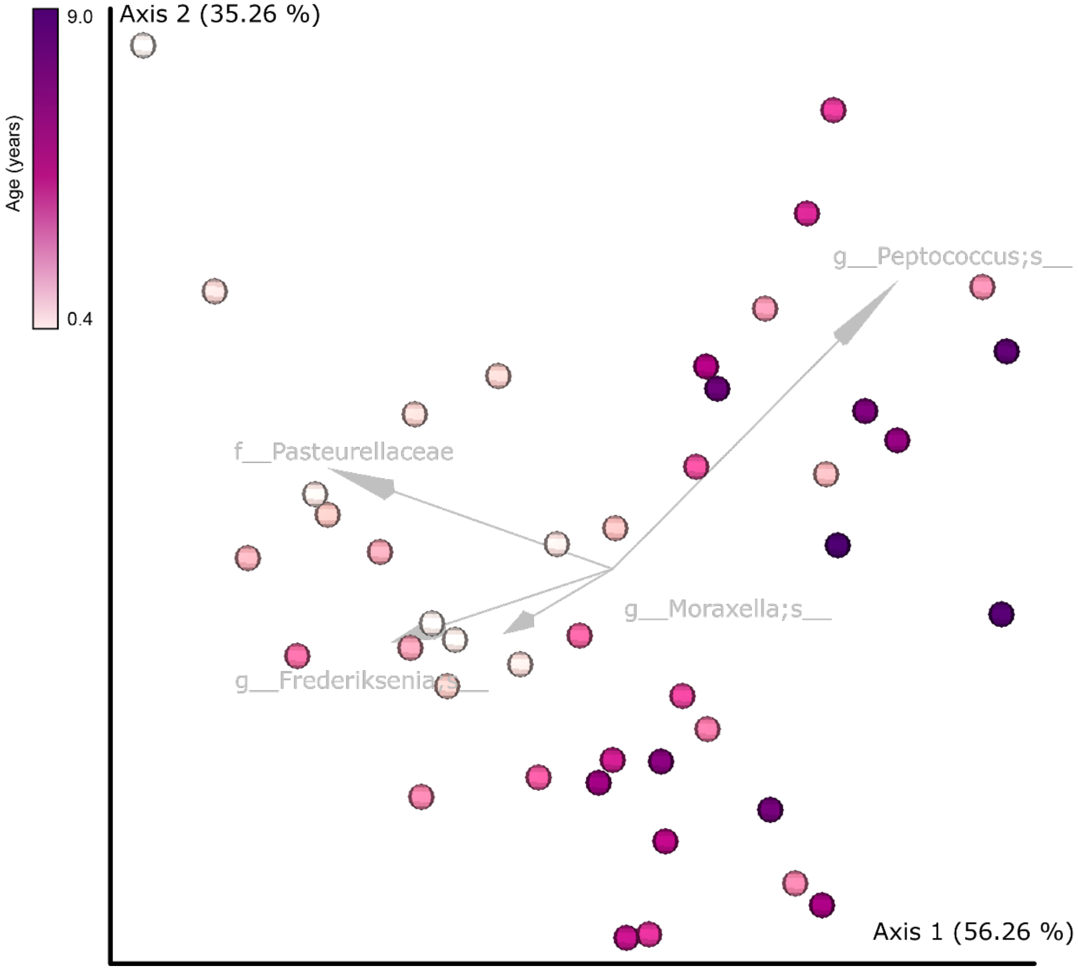

Figure **6-3**: Principal Coordinates Analysis (PCoA) biplot showing the first two axes of Aitchison beta diversity among oral microbiome samples from dogs (n = 43) in relation to age. Each point represents an individual dog, with proximity on the plot indicating greater similarity in microbial composition.

After assessing demographic and processing factors, oral microbiome beta diversity was subsequently analyzed against metadata variables related to stress and social behavior. After controlling for sequencing batch, the MCPQ-R survey dimension of neuroticism was not significantly associated with the composition of the oral microbiome (PERMANOVA, $F = 0.848$, $n = 43$, $p = 0.459$), nor was salivary cortisol concentration (PERMANOVA, $F = 0.076$, $n = 40$, $p = 0.976$) or hair cortisol concentration (PERMANOVA, $F = 2.078$, $n = 41$, $p = 0.129$). The beta diversity of the oral microbiome also did not differ between dogs who ate the food in the umbrella temperament task and those who did not (PERMANOVA, *F* = 0.128, *n* = 37, *p* = 0.912). However, a significant difference was observed in beta diversity of dogs that lived with another dog in the household and those that did not (PERMANOVA, *F* = 3.146, *n* = 43, *p* = 0.036, Figure 6-4).

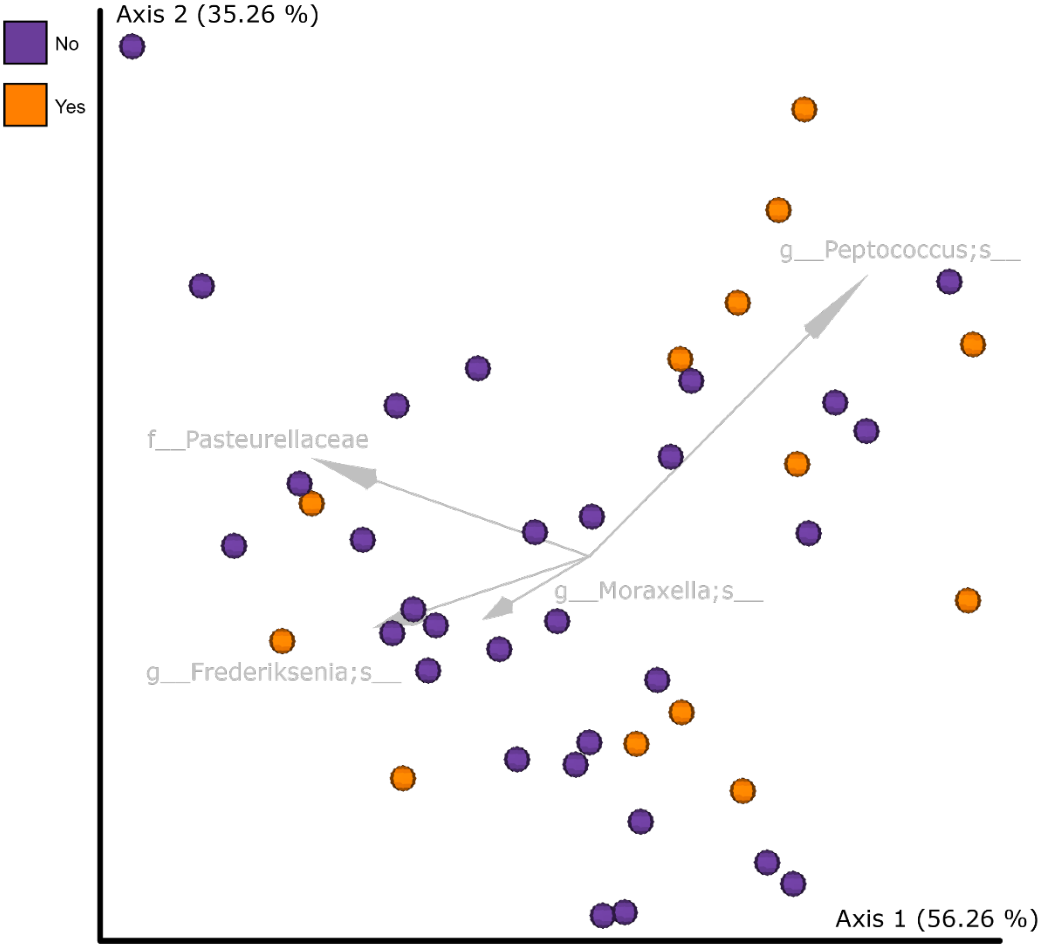

Figure **6-4**: Principal Coordinates Analysis (PCoA) biplot showing the first two axes of Aitchison beta diversity among oral microbiome samples from dogs (*n* = 43) in relation to the presence or absence of other dogs in the household. Each point represents an individual dog, with proximity on the plot indicating greater similarity in microbial composition. Dogs that live with another dog (“yes”) are indicated in orange.

MaAsLin2 was used to identify ASVs that differed in abundance between the oral microbiomes of dogs based on the aforementioned variables. Three ASVs were significantly associated with sequencing batch. Specifically, the second batch had higher abundances of

Saccharimonadaceae TM7 species ($\beta = 2.965$, $p = 9.153\times10^{-7}$, $q = 1.465\times10^{-4}$), an *Actinomyces* species ($\beta = 1.959$, $p = 9.352\times10^{-5}$, $q = 7.481\times10^{-3}$), and an unspecified Bacteria ($\beta = 1.479$, $p = 5.243\times10^{-4}$, $q = 0.028$). Therefore, sequencing batch was included as a random effects variable in subsequent analyses. No differentially abundant oral ASVs were found based on sex, spay/neuter status, salivary or hair cortisol concentration, MCPQ-R neuroticism rating, umbrella temperament task performance, or the presence of other dogs in the household. However, 100 ASVs were differentially abundant in the oral microbiome based on age (Appendix M). The three ASVs with the largest significant associations with age included: a *Streptobacillus* species ($\beta = -1.755$, $p = 8.135\times10^{-6}$, $q = 2.190\times10^{-4}$), a *Flexilinea* species ($\beta = 1.660$, $p = 7.476\times10^{-8}$, $q = 1.196\times10^{-5}$), and a Christensenellaceae R.7 group species ($\beta = 1.644$, $p = 1.344\times10^{-5}$, $q = 2.190\times10^{-4}$).

The Shannon alpha diversity of the oral microbiome samples was not significantly different between the two sequencing batches (Kruskal-Wallis test, $H = 2.182$, $n = 43$, $p = 0.140$). No significant alpha diversity differences were observed based on sex (Kruskal-Wallis test, $H = 0.401$, $n = 43$, $p = 0.527$) or spay/neuter status (Kruskal-Wallis test, $H = 2.736$, $n = 43$, $p = 0.098$). However, the Shannon alpha diversity of the oral microbiome was significantly and positively correlated with age (Spearman's correlation test, $r = 0.591$, $n = 43$, $p < 0.0001$, Figure 6-5).

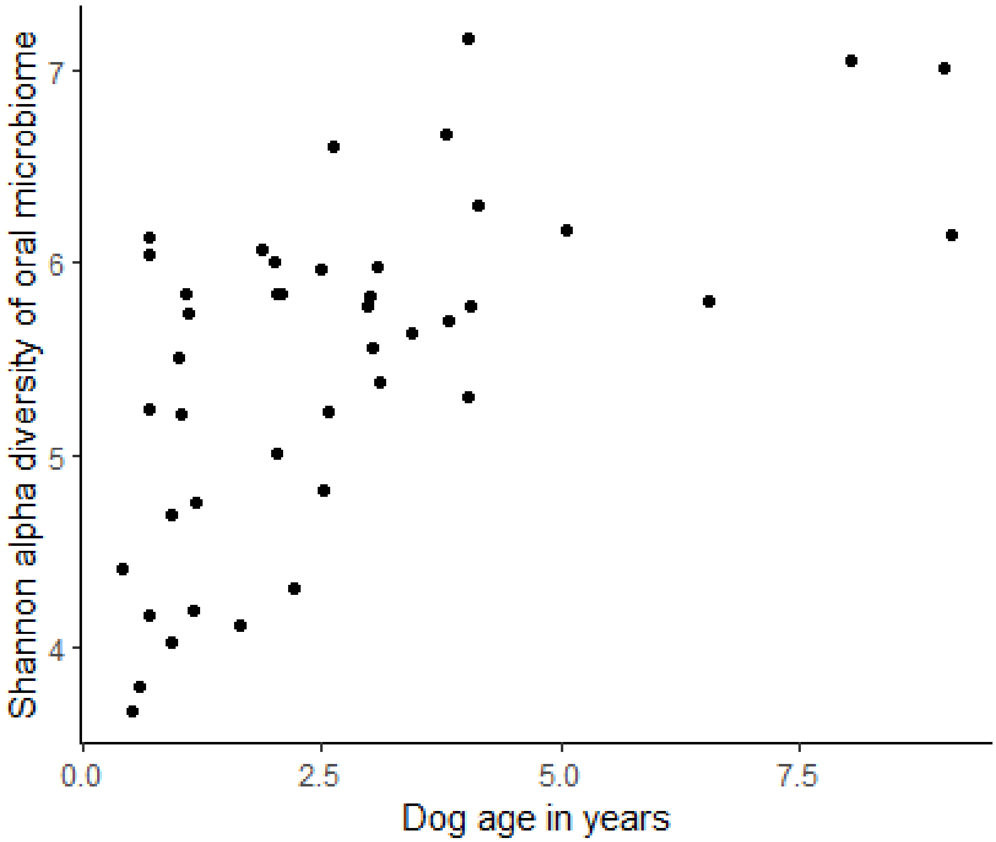

Figure **6-5**: Relationship between Shannon alpha diversity (at the ASV level) of the oral microbiome and age of dogs.

The alpha diversity of the oral microbiome samples did not differ in association with measures of stress. There was no significant correlation with the MCPQ-R neuroticism rating (Spearman's correlation test, $r = 0.276$, $n = 43$, $p = 0.073$), baseline salivary cortisol concentration (Spearman's correlation test, $r = 0.277$, $n = 40$, $p = 0.084$), hair cortisol concentration (Spearman's correlation test, $r = 0.092$, $n = 41$, $p = 0.568$), or whether the dog ate food during the umbrella temperament task (Kruskal-Wallis test, $H = 0.564$, $n = 37$, $p = 0.452$). There was also no difference in alpha diversity between dogs that lived with another dog and those that did not (Kruskal-Wallis test, $H = 2.193$, $n = 43$, $p = 0.139$).

Gut microbiome

The gut microbiome samples collected in this study were sequenced from 15 dogs, all in a single batch. The most abundant genera identified in the samples were *Peptoclostridium*, *Bacteroides*, *Prevotella* 9, *Catenibacterium*, and *Fusobacterium*. (Figure 6-6).

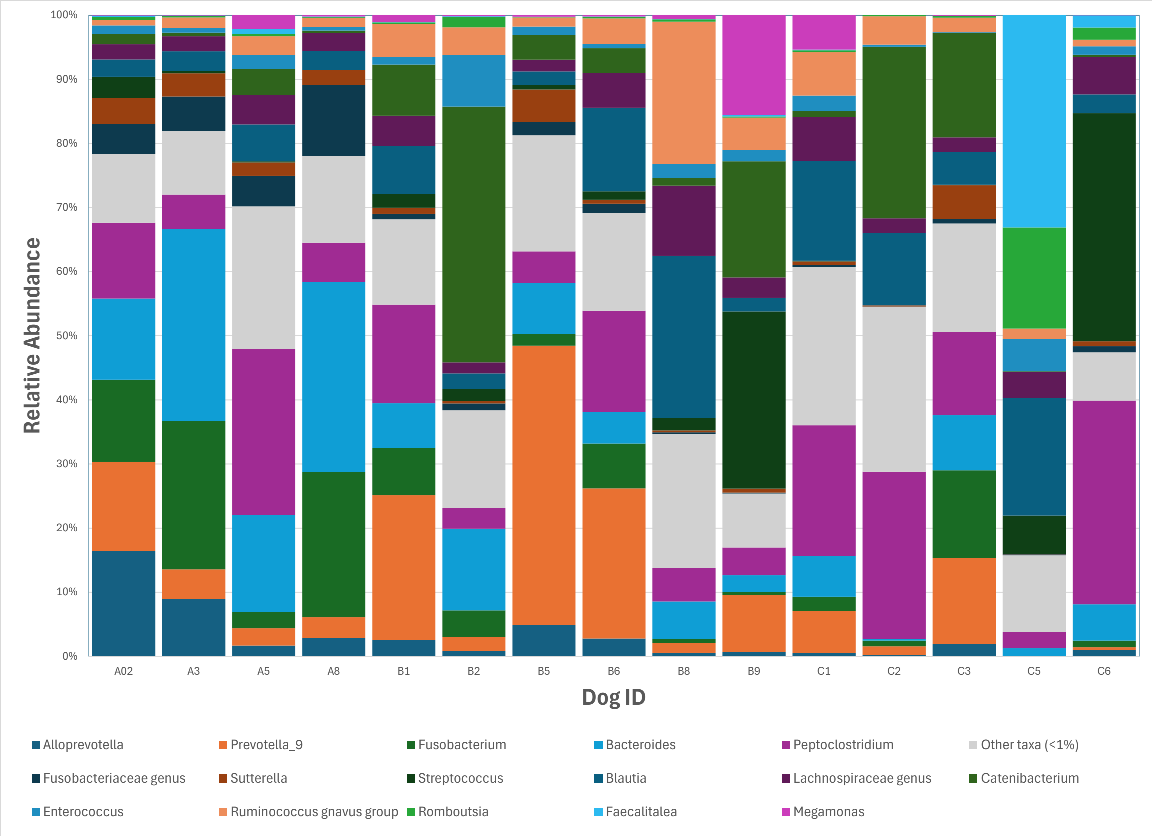

Figure **6-6**: Taxonomic barplot of the relative abundance of different genera detected using 16S sequencing in the gut microbiome samples of dogs in this study (n = 15). Dog IDs are shown on the x-axis. Genera representing less than 1% of the total abundance across all dogs are aggregated into the "Other taxa" category.

The beta diversity of the gut microbiome samples did not differ by sex (PERMANOVA, F = 0.356, n = 15, p = 0.735) or spay/neuter status (PERMANOVA, F = 1.223, n = 15, p = 0.336). Additionally, gut microbiome beta diversity was not significantly associated with age (PERMANOVA, F = 2.199, n = 15, p = 0.118).

The association of the gut microbiome beta diversity with markers of stress and social behavior was also examined. The beta diversity of the gut microbiome was not significantly associated with the neuroticism score from the MCPQ-R survey (PERMANOVA, F = 0.259, *n* = 15, *p* = 0.826), baseline salivary cortisol concentrations (PERMANOVA, F = 0.551, *n* = 15, *p* = 0.669), or hair cortisol concentration (PERMANOVA, F = 3.336, *n* = 13, *p* = 0.054). However, a significant difference was found between dogs that ate the food in the temperament task and those that did not (PERMANOVA, F = 4.113, *n* = 13, *p* = 0.014, Figure 6-7). The gut microbiome beta diversity was not associated with whether there were other dogs living in the same household (PERMANOVA, F = 1.201, *n* = 15, *p* = 0.371).

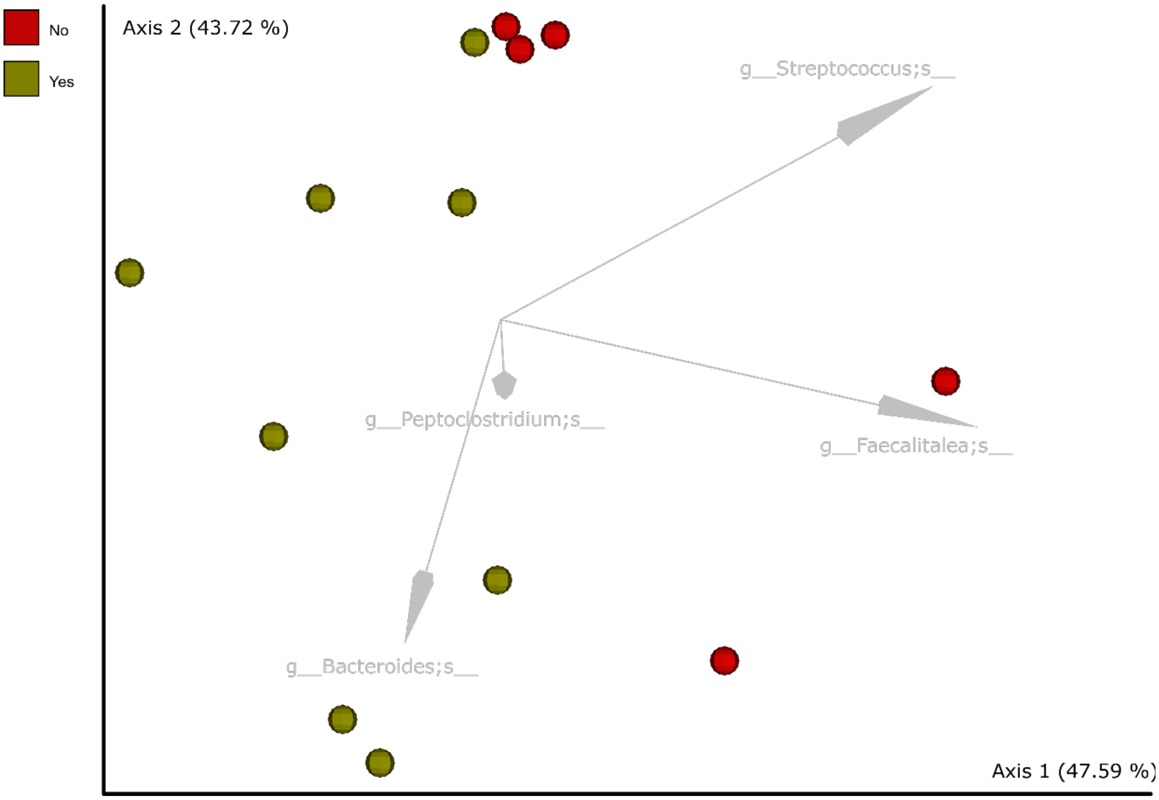

Figure **6-7**: Biplot depicting the first two Principal Coordinates of Analysis (PCoA) of the gut microbiomes of the dogs sampled in this study (*n* = 13) in relation to the temperament task. Dogs with more similar Aitchison's beta diversity are depicted closer together on the plot. Dogs that consumed the treat during the umbrella temperament task ("yes") are indicated in yellow.

To test for differences in ASVs between dogs' gut microbiomes, MaAsLin2 was used to examine associations with the variables mentioned above. No taxa were found to be differentially abundant in the gut microbiomes of dogs based on sex, spay/neuter status, age, salivary or hair cortisol concentrations, MCPQ-R neuroticism rating, umbrella temperament task performance, or the presence of another dog in the household.

For gut microbiome samples, the Shannon alpha diversity of dogs was not significantly associated with sex (Kruskal-Wallis test, $H = 0.000$, $n = 15$, $p = 1.000$), spay/neuter status (Kruskal-Wallis test, $H = 0.000$, $n = 15$, $p = 1.000$), or age (Spearman's correlation test, $r = 0.093$, $n = 15$, $p = 0.742$). There was no association of alpha diversity with MCPQ-R neuroticism rating (Spearman's correlation test, $r = 0.043$, $n = 15$, $p = 0.878$), baseline salivary cortisol concentration (Spearman's correlation test, $r = 0.071$, $n = 15$, $p = 0.800$), hair cortisol concentration (Spearman's correlation test, $r = 0.165$, $n = 13$, $p = 0.591$), or the results of the umbrella temperament task (Kruskal-Wallis test, $H = 1.736$, $n = 13$, $p = 0.188$). Alpha diversity did not differ based on whether dogs lived with another dog in the household (Kruskal-Wallis test, $H = 0.681$, $n = 15$, $p = 0.409$).

Wolf-dog comparisons

The oral microbiome samples in this study were compared to wolf and dog samples published by Podar et al. (2024). When our samples were pooled with these samples, the beta diversity of oral microbiome samples was significantly different between dogs and wolves (PERMANOVA, $F = 7.542$, $n = 75$, $p = 0.001$, Figure 6-8). As methodological differences between studies could contribute differences in beta diversity, a PERMANOVA was also run with both the host species and study as predictors, finding a significant effect of both study ($F = 3.408$, $p = 0.022$) and host species ($F = 7.794$, $p = 0.003$) when considered in the same model. To identify which genera of bacteria were differentially abundant between dogs and wolves, MaAsLin2 was used to detect those genera that significantly differed between host species, with the study as a random effects variable (Appendix N). There were 35 genera found to significantly differ between wolf and dog oral microbiomes after controlling for study. The top three genera significantly more common in wolf oral microbiomes than dog oral microbiomes by effect size were a *Clostridiaceae* genus ($\beta = 5.898$, $p = 1.045\times10^{-20}$, $q = 1.672\times10^{-18}$), *Pseudomonas* ($\beta = 3.509$, $p = 2.536\times10^{-10}$, $q = 2.028\times10^{-8}$), and *Acinetobacter* ($\beta = 3.093$, $p = 5.901\times10^{-6}$, $q = 1.349\times10^{-4}$). The top three genera significantly more common in dog oral microbiomes than wolf microbiomes by effect size were a *Treponema* ($\beta = -3.233$, $p = 2.794\times10^{-5}$, $q = 4.100\times10^{-4}$), *Absconditabacteriales* SR1 ($\beta = -3.085$, $p = 1.954\times10^{-5}$, $q = 3.697\times10^{-4}$), and *Fretibacterium* ($\beta = -2.863$, $p = 1.565\times10^{-4}$, $q = 1.391\times10^{-3}$).

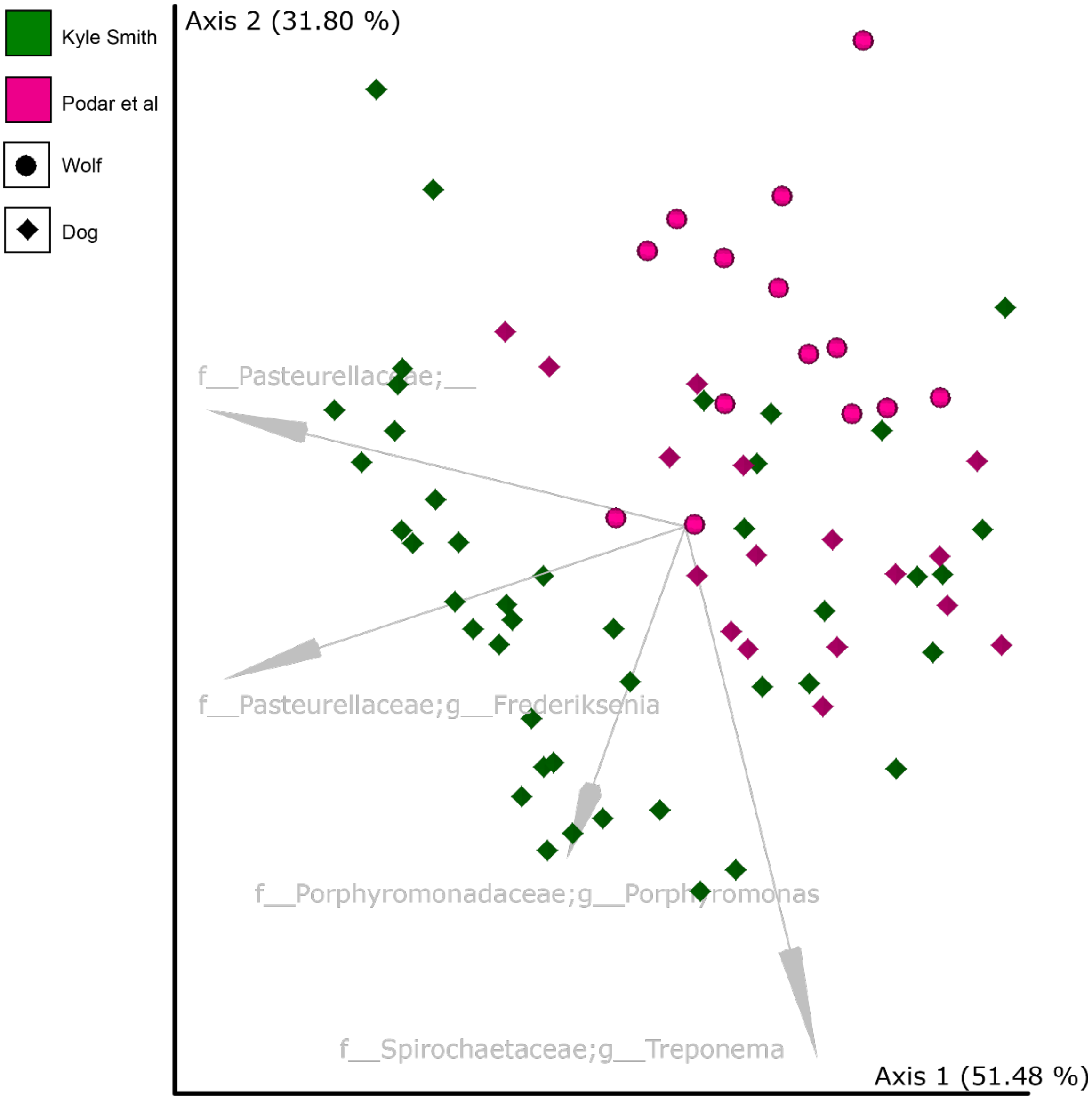

Figure **6-8**: Biplot depicting the first two Principal Coordinates of Analysis of the oral microbiomes of the dogs and wolves in this study and two others. Dogs with more similar Aitchison's beta diversity are depicted closer together on the plot. Dogs are indicated with diamonds and wolves are indicated with circles. Samples from this study are in green and from Podar et al. (2024) in pink.

For the gut microbiome samples, comparisons were made to samples from Reese et al. (2021) and Xu et al. (2021), both of whom had published samples from dogs and wolves. Considering only whether the host species was a dog or wolf, there was a significant difference in gut microbiome beta diversity between host species (PERMANOVA, F = 10.067, n = 62,

$p = 0.001$, Figure 6-9). To address possible methodological differences between studies, the PERMANOVA was rerun with the study as a covariate, finding an effect of both the study ($F = 18.510$, $p = 0.001$) and host species ($F = 15.943$, $p = 0.001$). To characterize the genera that differed between wolves and dogs, MaAsLin2 was used to test for a host species difference, controlling for study, finding 35 genera that differed between the dog and wolf gut microbiomes (Appendix O). The top three genera significantly more common in wolf gut microbiomes by effect size were a *Fusobacteriaceae* genus ($\beta = 2.998$, $p = 1.744\times10^{-5}$, $q = 2.456\times10^{-4}$), *Ruminococcus* torques group ($\beta = 2.476$, $p = 1.333\times10^{-8}$, $q = 3.754\times10^{-7}$), and *Oribacterium* ($\beta = 2.054$, $p = 3.235\times10^{-6}$, $q = 5.467\times10^{-5}$). The top three genera significantly more common in dog oral microbiomes by effect size were a *Lactobacillaceae* HT002 ($\beta = -5.511$, $p = 1.685\times10^{-12}$, $q = 2.847\times10^{-10}$), *Lactobacillus* ($\beta = -4.949$, $p = 2.846\times10^{-10}$, $q = 1.815\times10^{-8}$), and another *Lactobacillaceae* genus ($\beta = -4.734$, $p = 2.729\times10^{-9}$, $q = 1.153\times10^{-7}$).

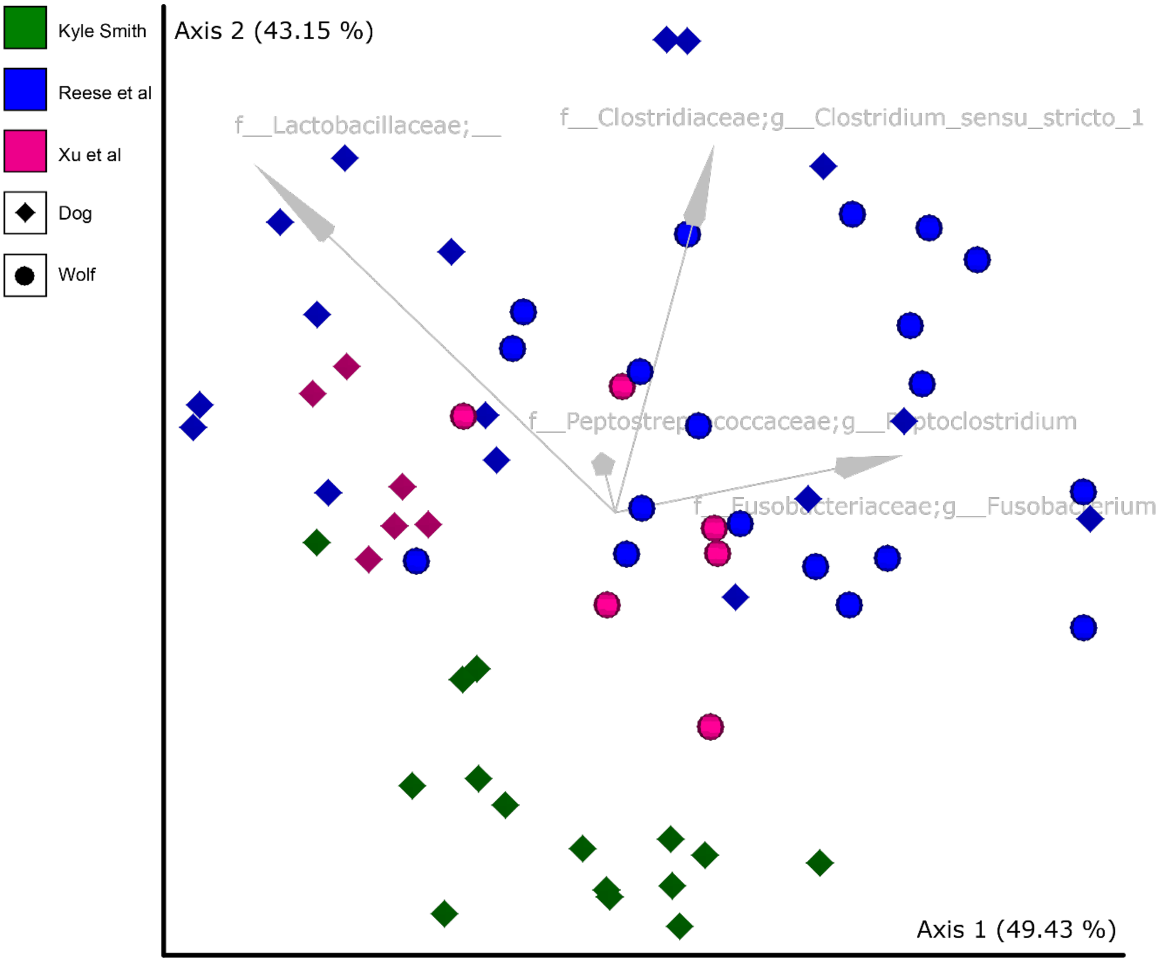

Figure **6-9**: Biplot showing the first two Principal Coordinates of Analysis of gut microbiome beta diversity among dogs and wolves from this study and two others. Samples with more similar Aitchison beta diversity are plotted closer together. Dogs are indicated with diamonds and wolves with circles. Samples from this study are in green, those from Xu et al. (2021) in pink, and those from Reese et al. (2021) in blue.

Discussion

The microbiome is of interest for understanding dog domestication and the factors affecting dogs' health. Animal domestication is linked to shifts in the microbiome, which is likely related to diet, among other factors (Reese et al., 2021; J. Xu et al., 2021). Within dogs, chronic stress (Dreschel, 2010) and social relationships (McCoy et al., 2023) are linked to differences in health. As the microbiome has been linked to social behavior and stress in humans and mice (Dill-McFarland et al., 2019; Sarkar et al., 2024; Tofani et al., 2024; Wu et al., 2021), these relationships are worth exploring in dogs as a possible mechanism linking these factors to health.

This study examined how the oral and gut microbiomes of companion dogs in the United States relate to demographic, stress-related, and social factors, and compared these microbiomes to those of dogs and wolves from published studies. Age had a strong and consistent effect on the oral microbiome across all metrics: Shannon alpha diversity, Aitchison beta diversity, and differential abundance analysis. Older dogs had greater microbial diversity and distinct taxa in their oral microbiomes, with 100 ASVs significantly associated with age. Spay/neuter status was also associated with oral microbiome beta diversity, though this may reflect age differences rather than a direct effect. Most stress- and social-related traits were not significantly associated with microbiome composition. Exceptions included a difference in oral beta diversity based on whether a dog lived with another dog, and a gut microbiome beta diversity difference depending on whether the dog consumed a treat after a temperament challenge. Comparative analysis revealed clear differences in microbiome composition between dogs and wolves, both in the oral and gut microbiomes, even after accounting for study-specific variation. These differences spanned overall beta diversity and multiple bacterial genera.

In this study, we advance our understanding of microbiome differences between dogs and wolves by comparing these samples to the published literature. For the oral microbiome, we contributed a substantially larger sample of pet dogs to an existing dataset comparing dogs and wolves (Podar et al., 2024), and we merged two existing studies of the gut microbiomes of dogs and wolves (Reese et al., 2021; J. Xu et al., 2021) and added a modest number of additional dogs. For both the oral and gut microbiomes, there were significant beta diversity differences between studies after controlling for host species. There are multiple possible causes of these study effects, which could reflect either real differences in the microbiomes of these populations or methodological effects. The dogs in this study and some of the dogs compared to in the published literature were pets, but there were also dogs living at a research facility kennel in one gut microbiome study (J. Xu et al., 2021). Wolf populations studied included wolves in the wild (Podar et al., 2024), at a zoo (J. Xu et al., 2021), and at a wildlife sanctuary (Reese et al., 2021), resulting in distinct diets, environmental exposures, and stressors. Unfortunately, limited demographic metadata in the published datasets prevented us from controlling for important variables such as age, sex, or diet. Beyond population-level variation, methodological differences may also have contributed to study effects. For instance, Podar et al. collected oral swabs from both gums and dental plaque, whereas our samples were taken from the gums and inner cheeks (Podar et al., 2024). In the gut microbiome data, our samples were thawed and buffered before sequencing, while the other studies did not specify this step. Differences in DNA extraction methods, sequencing platforms, or potential lab-specific contaminants could also introduce variation. Together, these considerations highlight the importance of harmonizing both metadata collection and laboratory protocols in future comparative microbiome studies.

Nevertheless, even after controlling for study-specific effects, there were clear average differences in the composition of both the gut and oral microbiomes of dogs and wolves. Overall beta diversity differed, and 35 genera each in the oral and gut microbiomes were found to be differentially abundant between dogs and wolves. It is particularly noteworthy that in the gut microbiome, the three genera with the largest effect sizes that were significantly more common in dogs than wolves were *Lactobacillus* and two other *Lactobacillaceae* genera. *Lactobacillus* can break down lactose (Premi et al., 1972), which is a function that most adult mammals lack (Campbell et al., 2009). In contrast, some human populations have evolved persistent lactase activity into adulthood in societies where dairy is a dietary staple (Ségurel & Bon, 2017). Dogs in some parts of the world, especially Europe and the Middle East, have also undergone selection on an allele of the lactase gene, and in vitro experiments suggest that this increases the expression of this gene (Y. H. Liu et al., 2021). Dogs in regions or households where dairy is consumed have been found to harbor greater diversity of *Lactobacillus* species in their guts (Yarlagadda et al., 2022). Given that dogs often consume diets similar to those of nearby humans (Guiry, 2012, 2013) and have in some cases undergone convergent evolution with humans to digest human-associated foods (Axelsson et al., 2013; Y. H. Liu et al., 2021), the enrichment of *Lactobacillus* in dog gut microbiomes may represent a functional adaptation facilitated by the microbiota.

These findings, viewed in combination with other work, suggest a model for the evolution of new dietary adaptations that could apply to both humans and dogs and be more easily tested using data from both species. A study using ancient DNA from coprolites of Bronze Age Italian dogs found that the dogs' own amylase genes had not yet increased in copy number to the level seen in modern European dog breeds, but the enrichment of alpha-amylase genes in the gut microbiomes were at levels well above that of wolves and modern dogs (Rampelli et al., 2021). As the composition of the microbiome can change more quickly than the genetic evolution of a whole population of mammals, perhaps the microbiome can provide a way for a species to initially be able to digest a new diet different from that which its ancestors evolved to consume. Then, this allows for the sustained consumption of this diet, enabling selection to be able to act on the underlying genetic variation and any new mutations. *Lactobacillus* could be playing this role in the case of lactose consumption, which is very unusual for most adult mammals. While there is some recent evidence of selection on an allele of lactase in dogs that is believed to increase expression of this gene (Y. H. Liu et al., 2021), no in vivo research has yet clarified the degree to which this affects dogs' ability to digest milk. Like the Bronze Age dogs that nevertheless had some copies of amylase genes, perhaps this mutation has improved dogs' ability to digest dairy, and the microbiome is helping buffer this. Also, as there is variation in this gene within the dog population, it is possible that *Lactobacillus* exists at higher abundance in dogs who are not lactase persistent but still consume dairy. A similar effect is seen in humans, where people who eat dairy but are not genetically lactase persistent have higher levels of *Bifidobacteria*, which help digest lactose (Goodrich et al., 2017). Future research should examine the relationship between dogs' and humans' diet, genetic adaptations, and functional characteristics of their microbiomes. This could also help clarify some unsolved mysteries, such as why selection on lactase persistence in Europe occurred thousands of years after widespread dairy consumption (Evershed et al., 2022) or why some modern populations have low levels of lactase persistence despite a long history of dairy consumption (Segurel et al., 2020). Selection on the lactase gene is estimated to have occurred far earlier in European dogs than in European humans (Y. H. Liu et al., 2021), so research on ancient microbiomes or other hypothesized relevant factors, such as malnutrition or disease(Evershed et al., 2022), may help clarify the selective pressure that operated at different times in the two species. As noted in Chapter 2, dogs' widespread presence in human societies across space and time, as well as their evolutionary convergences with humans, make them particularly well-suited to test models of recent human evolution, such as dietary adaptations.

The major differences between domestic dogs and wolves include not only diet (Axelsson et al., 2013) but also the stress response and social cognition (Cagan & Blass, 2016; Salomons et al., 2021). Compared to wolves, dogs are less fearful and better at communicating with humans (Salomons et al., 2021). Within dogs, more fearful dogs are shorter lived (Dreschel, 2010) and dogs with more social support are in better health (McCoy et al., 2023). This aligns with the broader literature linking chronic stress to worse health outcomes (O'Connor et al., 2021; Yegorov et al., 2020) and strong social relationships to better health (Snyder-Mackler et al., 2020; Yang et al., 2016). As the microbiome represents a possible mechanism by which these factors can affect health, we decided to explore associations between dogs' microbiomes and factors related to stress and social relationships.

While this study found only limited evidence of associations between the microbiome and stress and social factors, these relationships warrant further exploration with larger sample sizes. The gut microbiome beta diversity differed based on performance in the umbrella temperament task, but caution is warranted when interpreting this finding, given the small sample size (*n* = 15) and the absence of similar associations in other stress proxies or in differential abundance analyses. Nevertheless, stress and social factors remain important to consider, especially in the context of aging and noncommunicable disease. Chronic stress has consistently been found to be associated with various chronic health conditions and shorter lifespans (O'Connor et al., 2021; Sapolsky, 2004), including in dogs (Dreschel, 2010). This may be related to chronic activation of the HPA axis (one of the stress responses) leading to long-term inflammation (Miller et al., 2002; O'Connor et al., 2021). Social relationships have also been linked to chronic health outcomes in humans and other species of social mammals (Snyder-Mackler et al., 2020). The microbiome has been linked to both stress (e.g., via stress hormone-microbe interactions) (Foster et al., 2017; Tanelian et al., 2022; C. Xu et al., 2020) and social behavior (e.g., through microbial sharing and immune regulation) (Carlson et al., 2021; Wu et al., 2021), suggesting it could be a key mediator between psychosocial environments and health. As such, future studies should continue to examine the microbiome as a potential biological pathway linking stress, social connectedness, and chronic disease risk, particularly in longitudinal designs that can capture changes across time and life stage.

The age-related changes observed in dogs' oral microbiomes in this study are consistent with emerging research and reveal intriguing contrasts with patterns observed in humans. For instance, Templeton et al., (2023) found no cross-sectional association between age and alpha diversity across ten dogs, but did observe longitudinal increases in diversity over two to three time points across two years (Templeton et al., 2023). While their study was limited to geriatric dogs (9.5-14.8 years of age), our cross-sectional study included a broader age range (under 1 year to 9 years) and a larger sample size (*n* = 43), which likely increased the power to detect age-related trends. Together, these findings suggest that the oral microbiome diversity in dogs may continue to accumulate throughout life, including during adulthood and into old age. Longitudinal studies that span the full canine lifespan—from puppyhood through senescence—are needed to map the trajectory of microbial changes over time. Interestingly, the age-related increase in oral microbiome alpha diversity in dogs contrasts with trends observed in humans. Liu et al. (2020) reported a decline in oral alpha diversity from adolescence through middle age in a human cohort, suggesting that microbial aging patterns may diverge significantly between species (S. Liu et al., 2020). In dogs, not only did the number of microbial taxa increase with age, but the overall community composition also shifted markedly, with 100 ASVs showing significant age associations. One interesting question for future investigation is whether these age-related changes in dogs' oral microbiomes are associated with shifts in diet, immune function, dental health, or behavior as dogs age. For example, older dogs may have altered oral environments due to changes in saliva production, immune regulation, or dental wear and disease—all factors that could shape microbial communities. Integrating longitudinal microbial, physiological, and behavioral data could help clarify the mechanisms driving these changes and their potential health implications.

The relationship between the oral microbiome and age in dogs is of particular scientific interest due to the well-established connections among aging, the microbiome, and chronic health outcomes. In humans living in industrialized countries, aging is the strongest risk factor for most major causes of death, including noncommunicable diseases (NCDs) such as type 2 diabetes, cardiovascular disease, cancer, and neurodegenerative conditions like Alzheimer's disease (Kaeberlein, 2013). While the incidence of NCDs is markedly higher in industrialized nations than in non-industrialized ones, the underlying causes of this disparity remain incompletely understood (Wagner & Brath, 2012). One potential explanatory factor is the human microbiome, which differs significantly between individuals living in industrialized and non-industrialized contexts (Jha et al., 2018; Mancabelli et al., 2017; Tian et al., 2025). These microbial differences are increasingly implicated in the etiology of numerous NCDs (Gancz & Weyrich, 2023), suggesting that the microbiome may play a role in the global rise of chronic diseases as societies undergo industrialization. Understanding how the microbiome shifts with age, particularly in industrialized contexts, could offer insight into why chronic disease risk increases with age and how interventions targeting the microbiome might help mitigate these risks. Companion dogs, who live alongside humans in industrialized environments and are affected by many of the same age-related conditions, offer a valuable model for studying these questions. Tracking how their microbiomes change with age may reveal generalizable patterns relevant to both veterinary and human medicine, especially as we seek to understand how lifestyle and environmental exposures shape aging and disease through the microbiome.

Dogs may serve as an especially valuable model organism for studying the relationship between the microbiome, aging, noncommunicable diseases, and lifestyle. In the United States, dogs and humans share similar mortality patterns for many leading causes of death, as well as comparable age-related health trajectories and levels of comorbidity across chronic diseases (Hoffman et al., 2018). Both species also experience variability in lifestyle factors known to influence long-term health outcomes—including diet, physical activity, climate, chemical exposures, and access to healthcare. However, dogs' accelerated lifespans allow researchers to study the impacts of these environmental and behavioral factors on aging and chronic disease risk over shorter time frames, making them a promising model for aging research (Hoffman et al., 2018; Ruple et al., 2022). Moreover, parallels between humans and dogs extend to the microbiome. As with humans, dogs living in rural, non-industrialized environments tend to have more diverse gut microbiomes than those living in urban, industrialized settings (Yarlagadda et al., 2022). Differences in microbiome composition between dogs and their wild relatives (e.g., wolves) resemble the divergence observed between industrialized and non-industrialized human populations (Reese et al., 2021). These patterns suggest that dogs, like humans, exhibit microbiome signatures shaped by industrialization, making them a particularly relevant model for exploring how modern environments influence microbiome-associated disease. Future research should explore how microbiome composition correlates with chronic health outcomes in aging dogs and how these associations compare to those observed in humans—especially in relation to lifestyle and environmental exposures linked to industrialization. Longitudinal efforts such as the Dog Aging Project, which collects extensive health, environmental, and microbiome data from a large population of companion dogs (Kaeberlein et al., 2016), offer a valuable resource for investigating whether patterns seen in human aging and disease are mirrored in dogs. Such comparative approaches could help uncover fundamental mechanisms underlying the microbiome's role in health and aging across species.

References

Archie, E. A., & Tung, J. (2015). Social behavior and the microbiome. *Current Opinion in Behavioral Sciences*, *6*, 28–34. https://doi.org/10.1016/j.cobeha.2015.07.008

Axelsson, E., Ratnakumar, A., Arendt, M. L., Maqbool, K., Webster, M. T., Perloski, M., Liberg, O., Arnemo, J. M., Hedhammar, Å., & Lindblad-Toh, K. (2013). The genomic signature of dog domestication reveals adaptation to a starch-rich diet. *Nature*, *495*(7441), 360–364. https://doi.org/10.1038/nature11837

Bäckhed, F., Fraser, C. M., Ringel, Y., Sanders, M. E., Sartor, R. B., Sherman, P. M., Versalovic, J., Young, V., & Finlay, B. B. (2012). Defining a healthy human gut microbiome: current concepts, future directions, and clinical applications. *Cell Host and Microbe*, *12*(5), 611–622. https://doi.org/10.1016/j.chom.2012.10.012

Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rates: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society: Series B (Methodological)*, *57*(1), 289–300. https://doi.org/10.1353/aad.2012.0408

Bolyen, E., Rideout, J. R., Dillon, M. R., Bokulich, N. A., Abnet, C. C., Al-Ghalith, G. A., Alexander, H., Alm, E. J., Arumugam, M., Asnicar, F., Bai, Y., Bisanz, J. E., Bittinger, K., Brejnrod, A., Brislawn, C. J., Brown, C. T., Callahan, B. J., Caraballo-Rodríguez, A. M., Chase, J., … Caporaso, J. G. (2019). Reproducible, interactive, scalable and extensible microbiome data science using QIIME 2. *Nature Biotechnology*, *37*(8), 852–857. https://doi.org/10.1038/s41587-019-0209-9

Bray, E. E., Gruen, M. E., Gnanadesikan, G. E., Horschler, D. J., Levy, K. M., Kennedy, B. S., Hare, B. A., & MacLean, E. L. (2020). Cognitive characteristics of 8-to-10-week-old assistance dog puppies. *Animal Behaviour*, *166*, 193–206. https://doi.org/10.1016/j.anbehav.2020.05.019

Cagan, A., & Blass, T. (2016). Identification of genomic variants putatively targeted by selection during dog domestication. *BMC Evolutionary Biology*, *16*(1), 1–13. https://doi.org/10.1186/s12862-015-0579-7

Callahan, B. J., McMurdie, P. J., Rosen, M. J., Han, A. W., Johnson, A. J. A., & Holmes, S. P. (2016). DADA2: high-resolution sample inference from Illumina amplicon data. *Nature Methods*, *13*(7), 581–583. https://doi.org/10.1038/nmeth.3869

Campbell, A. K., Waud, J. P., & Matthews, S. B. (2009). The molecular basis of lactose intolerance. In *Science Progress* (Vol. 92, Issues 3–4). https://doi.org/10.3184/003685009X12547510332240

Carlson, A. L., Xia, K., Azcarate-Peril, M. A., Rosin, S. P., Fine, J. P., Mu, W., Zopp, J. B., Kimmel, M. C., Styner, M. A., Thompson, A. L., Propper, C. B., & Knickmeyer, R. C. (2021). Infant gut microbiome composition is associated with non-social fear behavior in a pilot study. *Nature Communications*, *12*(1), 1–16. https://doi.org/10.1038/s41467-021-23281-y

Davis, N. M., Proctor, Di. M., Holmes, S. P., Relman, D. A., & Callahan, B. J. (2018). Simple statistical identification and removal of contaminant sequences in marker-gene and metagenomics data. *Microbiome*, *6*(1), 1–14. https://doi.org/10.1186/s40168-018-0605-2

Dill-McFarland, K. A., Tang, Z. Z., Kemis, J. H., Kerby, R. L., Chen, G., Palloni, A., Sorenson, T., Rey, F. E., & Herd, P. (2019). Close social relationships correlate with human gut microbiota composition. *Scientific Reports*, *9*(1), 1–10. https://doi.org/10.1038/s41598-018-37298-9

Dreschel, N. A. (2010). The effects of fear and anxiety on health and lifespan in pet dogs. *Applied Animal Behaviour Science*, *125*(3–4), 157–162. https://doi.org/10.1016/j.applanim.2010.04.003

Evershed, R. P., Smith, G. D., Roffet-Salque, M., Timpson, A., Diekmann, Y., Lyon, M. S., Cramp, L. J. E., Casanova, E., Smyth, J., Whelton, H. L., Dunne, J., Brychova, V., Šoberl, L., Gerbault, P., Gillis, R. E., Heyd, V., Johnson, E., Kendall, I., Manning, K., … Thomas, M. G. (2022). Dairying, diseases and the evolution of lactase persistence in Europe. *Nature*, *608*(7922), 336–345.

Foster, J. A., Rinaman, L., & Cryan, J. F. (2017). Stress & the gut-brain axis: regulation by the microbiome. *Neurobiology of Stress*, *7*, 124–136. https://doi.org/10.1016/j.ynstr.2017.03.001

Gancz, A. S., & Weyrich, L. S. (2023). Studying ancient human oral microbiomes could yield insights into the evolutionary history of noncommunicable diseases. *F1000Research*, *12*, 109. https://doi.org/10.12688/f1000research.129036.1

Goodrich, J. K., Davenport, E. R., Clark, A. G., & Ley, R. E. (2017). The relationship between the human genome and microbiome comes into view. *Annual Review of Genetics*, *51*, 413–433. https://doi.org/10.1146/annurev-genet-110711-155532

Guiry, E. J. (2012). Dogs as analogs in stable isotope-based human paleodietary reconstructions: a review and considerations for future use. *Journal of Archaeological Method and Theory*, *19*(3), 351–376. https://doi.org/10.1007/s10816-011-9118-z

Guiry, E. J. (2013). A canine surrogacy approach to human paleodietary bone chemistry: Past development and future directions. *Archaeological and Anthropological Sciences*, *5*(3), 275–286. https://doi.org/10.1007/s12520-013-0133-8

Hoffman, J. M., Creevy, K. E., Franks, A., O'Neill, D. G., & Promislow, D. E. L. (2018). The companion dog as a model for human aging and mortality. *Aging Cell*, *17*(3). https://doi.org/10.1111/acel.12737

Hou, K., Wu, Z. X., Chen, X. Y., Wang, J. Q., Zhang, D., Xiao, C., Zhu, D., Koya, J. B., Wei, L., Li, J., & Chen, Z. S. (2022). Microbiota in health and diseases. *Signal Transduction and Targeted Therapy*, *7*(1). https://doi.org/10.1038/s41392-022-00974-4

Jha, A. R. (n.d.). *personal communication*.

Jha, A. R., Davenport, E. R., Gautam, Y., Bhandari, D., Tandukar, S., Ng, K. M., Fragiadakis, G. K., Holmes, S., Gautam, G. P., Leach, J., Sherchand, J. B., Bustamante, C. D., & Sonnenburg, J. L. (2018). Gut microbiome transition across a lifestyle gradient in Himalaya. *PLoS Biology*, *16*(11), 1–30. https://doi.org/10.1371/journal.pbio.2005396

Kaeberlein, M. (2013). Longevity and aging. *F1000Prime Reports*, *5*(March), 1–8. https://doi.org/10.12703/P5-5

Kaeberlein, M., Creevy, K. E., & Promislow, D. E. L. (2016). The Dog Aging Project: translational geroscience in companion animals. *Mammalian Genome*, *27*(7–8), 279–288. https://doi.org/10.1007/s00335-016-9638-7.The

Kennedy, M. S., & Chang, E. B. (2020). The microbiome: composition and locations. *Progress in Molecular Biology and Translational Science*, *176*, 1–42. https://doi.org/10.1016/bs.pmbts.2020.08.013

Kirchoff, N. S., Udell, M. A. R., & Sharpton, T. J. (2019). The gut microbiome correlates with conspecific aggression in a small population of rescued dogs (Canis familiaris). *PeerJ*, *2019*(1). https://doi.org/10.7717/peerj.6103

Ley, J. M., Bennett, P. C., & Coleman, G. J. (2008). A refinement and validation of the Monash Canine Personality Questionnaire (MCPQ). *Applied Animal Behaviour Science*, *116*, 220–227. https://doi.org/10.1016/j.applanim.2008.09.009

Liu, J., Tan, Y., Cheng, H., Zhang, D., Feng, W., & Peng, C. (2022). Functions of gut microbiota metabolites, current status and future perspectives. *Aging and Disease*, *13*(4), 1106–1126. https://doi.org/10.14336/AD.2022.0104

Liu, S., Wang, Y., Zhao, L., Sun, X., & Feng, Q. (2020). Microbiome succession with increasing age in three oral sites. *Ageing*, *12*(9), 7874–7907.

Liu, Y. H., Wang, L., Zhang, Z., Otecko, N. O., Khederzadeh, S., Dai, Y., Liang, B., Wang, G. D., & Zhang, Y. P. (2021). Whole-genome sequencing reveals lactase persistence adaptation in European dogs. *Molecular Biology and Evolution*, *38*(11), 4884–4890. https://doi.org/10.1093/molbev/msab214

Madhogaria, B., Bhowmik, P., & Kundu, A. (2022). Correlation between human gut microbiome and diseases. *Infectious Medicine*, *1*(3), 180–191. https://doi.org/10.1016/j.imj.2022.08.004

Mallick, H., Rahnavard, A., McIver, L. J., Ma, S., Zhang, Y., Nguyen, L. H., Tickle, T. L., Weingart, G., Ren, B., Schwager, E. H., Chatterjee, S., Thompson, K. N., Wilkinson, J. E., Subramanian, A., Lu, Y., Waldron, L., Paulson, J. N., Franzosa, E. A., Bravo, H. C., & Huttenhower, C. (2021). Multivariable association discovery in population-scale meta-omics studies. *PLoS Computational Biology*, *17*(11), 1–27. https://doi.org/10.1371/journal.pcbi.1009442

Mancabelli, L., Milani, C., Lugli, G. A., Turroni, F., Ferrario, C., van Sinderen, D., & Ventura, M. (2017). Meta-analysis of the human gut microbiome from urbanized and pre-agricultural populations. *Environmental Microbiology*, *19*(4), 1379–1390. https://doi.org/10.1111/1462-2920.13692

Mansour, S. R., Moustafa, M. A. A., Saad, B. M., Hamed, R., & Moustafa, A. R. A. (2021). Impact of diet on human gut microbiome and disease risk. *New Microbes and New Infections*, *41*, 100845. https://doi.org/10.1016/j.nmni.2021.100845

Martinez, K. B., Leone, V., & Chang, E. B. (2017). Microbial metabolites in health and disease: navigating the unknown in search of function. *Journal of Biological Chemistry*, *292*(21), 8553–8559. https://doi.org/10.1074/jbc.R116.752899

Martino, C., Shenhav, L., Marotz, C. A., Armstrong, G., McDonald, D., Vázquez-Baeza, Y., Morton, J. T., Jiang, L., Dominguez-Bello, M. G., Swafford, A. D., Halperin, E., & Knight, R. (2021). Context-aware dimensionality reduction deconvolutes gut microbial community dynamics. *Nature Biotechnology*, *39*(2), 165–168. https://doi.org/10.1038/s41587-020-0660-7

Marwaha, K., Cain, R., Asmis, K., Czaplinski, K., Holland, N., Mayer, D. C. G., & Chacon, J. (2025). Exploring the complex relationship between psychosocial stress and the gut microbiome: implications for inflammation and immune modulation. *Journal of Applied Physiology (Bethesda, Md. : 1985)*, *138*(2), 518–535. https://doi.org/10.1152/japplphysiol.00652.2024

McArdle, B. H., & Anderson, M. J. (2001). Fitting multivariate models to community data: A comment on distance-based redundancy analysis. *Ecology*, *82*(1), 290–297. https://doi.org/10.1890/0012-9658(2001)082[0290:FMMTCD]2.0.CO;2

McCoy, B. M., Brassington, L., Jin, K., Dolby, G. A., Shrager, S., Collins, D., Dunbar, M., Ruple, A., & Snyder-Mackler, N. (2023). Social determinants of health and disease in companion dogs: a cohort study from the Dog Aging Project. *Evolution, Medicine and Public Health*, *11*(1), 187–201. https://doi.org/10.1093/emph/eoad011

Miller, G. E., Cohen, S., & Ritchey, A. K. (2002). Chronic psychological stress and the regulation of pro-inflammatory cytokines: A glucocorticoid-resistance model. *Health Psychology*, *21*(6), 531–541. https://doi.org/10.1037/0278-6133.21.6.531

Mondo, E., Barone, M., Soverini, M., D'Amico, F., Cocchi, M., Petrulli, C., Mattioli, M., Marliani, G., Candela, M., & Accorsi, P. A. (2020). Gut microbiome structure and adrenocortical activity in dogs with aggressive and phobic behavioral disorders. *Heliyon*, *6*(1), e03311. https://doi.org/10.1016/j.heliyon.2020.e03311

O'Connor, D. B., Thayer, J. F., & Vedhara, K. (2021). Stress and health: a review of psychobiological processes. *Annual Review of Psychology*, *72*, 663–688. https://doi.org/10.1146/annurev-psych-062520-122331

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2018). *vegan: community ecology package*. https://cran.r-project.org/package=vegan

Pereira, A. M., & Clemente, A. (2021). Dogs' microbiome from tip to toe. *Topics in Companion Animal Medicine*, *45*, 100584. https://doi.org/10.1016/j.tcam.2021.100584

Perry, G. H., Dominy, N. J., Claw, K. G., Lee, A. S., Fiegler, H., Redon, R., Werner, J., Villanea, F. A., Mountain, J. L., Misra, R., Carter, N. P., Lee, C., & Stone, A. C. (2007). Diet and the evolution of human amylase gene copy number variation. *Nature Genetics*, *39*(10), 1256–1260. https://doi.org/10.1038/ng2123

Podar, N. A., Carrell, A. A., Cassidy, K. A., Klingeman, D. M., Yang, Z., Stahler, E. A., Smith, D. W., Stahler, D. R., & Podar, M. (2024). From wolves to humans: oral microbiome resistance to transfer across mammalian hosts. *MBio*, *15*(3). https://doi.org/10.1128/mbio.03342-23

Premi, L., Sandine, W. E., & Elliker, P. R. (1972). Lactose-hydrolyzing enzymes of Lactobacillus species. *Applied Microbiology*, *24*(1), 51–57. https://doi.org/10.1128/aem.24.1.51-57.1972

Quast, C., Pruesse, E., Yilmaz, P., Gerken, J., Schweer, T., Yarza, P., Peplies, J., & Glöckner, F. O. (2013). The SILVA ribosomal RNA gene database project: improved data processing and web-based tools. *Nucleic Acids Research*, *41*(D1), 590–596. https://doi.org/10.1093/nar/gks1219

R Core Team. (2023). *R: a language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.r-project.org

Rahman, S., O'connor, A. L., Becker, S. L., Patel, R. K., Martindale, R. G., & Tsikitis, V. L. (2023). Gut microbial metabolites and its impact on human health. *Annals of Gastroenterology*, *36*(4), 360–368. https://doi.org/10.20524/aog.2023.0809

Rampelli, S., Turroni, S., Debandi, F., Alberdi, A., Schnorr, S. L., Hofman, C. A., Taddia, A., Helg, R., Biagi, E., Brigidi, P., D'Amico, F., Cattani, M., & Candela, M. (2021). The gut microbiome buffers dietary adaptation in Bronze Age domesticated dogs. *IScience*, 135907. https://doi.org/10.1016/j.isci.2021.102816

Reese, A. T., Chadaideh, K. S., Diggins, C. E., Schell, L. D., Beckel, M., Callahan, P., Ryan, R., Thompson, M. E., & Carmody, R. N. (2021). Effects of domestication on the gut microbiota parallel those of human industrialization. *ELife*, *10*, 1–27. https://doi.org/10.7554/eLife.60197

Reiter, T., Jagoda, E., & Capellini, T. D. (2016). Dietary variation and evolution of gene copy number among dog breeds. *PLoS ONE*, *11*(2), 1–19. https://doi.org/10.1371/journal.pone.0148899

Ross, F. C., Patangia, D., Grimaud, G., Lavelle, A., Dempsey, E. M., Ross, R. P., & Stanton, C. (2024). The interplay between diet and the gut microbiome: implications for health and disease. *Nature Reviews Microbiology*, *22*(November). https://doi.org/10.1038/s41579-024-01068-4

Ruple, A., Maclean, E., Snyder-Mackler, N., Creevy, K. E., & Promislow, D. (2022). Dog models of aging. *Annual Review of Animal Biosciences*, *10*, 419–439. https://doi.org/10.1146/annurev-animal-051021-080937

Salomons, H., Smith, K. C. M., Callahan-Beckel, M., Callahan, M., Levy, K., Kennedy, B. S., Bray, E. E., Gnanadesikan, G. E., Horschler, D. J., Gruen, M., Tan, J., White, P., VonHoldt, B. M., MacLean, E. L., & Hare, B. (2021). Cooperative communication with humans evolved to emerge early in domestic dogs. *Current Biology*, *31*(July), 1–8. https://doi.org/10.1016/j.cub.2021.06.051

Sapolsky, R. M. (2004). Social status and health in humans and other animals. *Annual Review of Anthropology*, *33*(1), 393–418. https://doi.org/10.1146/annurev.anthro.33.070203.144000

Sarkar, A., McInroy, C. J. A., Harty, S., Raulo, A., Ibata, N. G. O., Valles-Colomer, M., Johnson, K. V. A., Brito, I. L., Henrich, J., Archie, E. A., Barreiro, L. B., Gazzaniga, F. S., Finlay, B. B., Koonin, E. V., Carmody, R. N., & Moeller, A. H. (2024). Microbial transmission in the social microbiome and host health and disease. *Cell*, *187*(1), 17–43. https://doi.org/10.1016/j.cell.2023.12.014

Ségurel, L., & Bon, C. (2017). On the evolution of lactase persistence in humans. *Annual Review of Genomics and Human Genetics*, *18*(April), 297–319. https://doi.org/10.1146/annurev-genom-091416-035340

Segurel, L., Guarino-Vignon, P., Marchi, N., Lafosse, S., Laurent, R., Bon, C., Fabre, A., Hegay, T., & Heyer, E. (2020). Why and when was lactase persistence selected for? Insights from Central Asian herders and ancient DNA. *PLoS Biology*, *18*(6), 1–11. https://doi.org/10.1371/journal.pbio.3000742

Snyder-Mackler, N., Burger, J. R., Gaydosh, L., Belsky, D. W., Noppert, G. A., Campos, F. A., Bartolomucci, A., Yang, Y. C., Aiello, A. E., O'Rand, A., Harris, K. M., Shively, C. A., Alberts, S. C., & Tung, J. (2020). Social determinants of health and survival in humans and other animals. *Science*, *368*(6493), eaax9553. https://doi.org/10.1126/science.aax9553

Song, S. J., Lauber, C., Costello, E. K., Lozupone, C. A., Humphrey, G., Berg-Lyons, D., Gregory Caporaso, J., Knights, D., Clemente, J. C., Nakielny, S., Gordon, J. I., Fierer, N., & Knight, R. (2013). Cohabiting family members share microbiota with one another and with their dogs. *ELife*, *2013*(2), 1–22. https://doi.org/10.7554/eLife.00458

Tanelian, A., Nankova, B., Miari, M., Nahvi, R. J., & Sabban, E. L. (2022). Resilience or susceptibility to traumatic stress: Potential influence of the microbiome. *Neurobiology of Stress*, *19*(May), 100461. https://doi.org/10.1016/j.ynstr.2022.100461

Templeton, G. B., Fefer, G., Case, B. C., Roach, J., Azcarate-Peril, M. A., Gruen, M. E., Callahan, B. J., & Olby, N. J. (2023). Longitudinal analysis of canine oral microbiome using whole genome sequencing in aging companion dogs. *Animals*, *13*(24). https://doi.org/10.3390/ani13243846

Tian, C., Zhang, T., Zhuang, D., Luo, Y., Li, T., Zhao, F., Sang, J., Tang, Z., Jiang, P., Zhang, T., Liu, P., Zhu, L., & Zhang, Z. (2025). Industrialization drives the gut microbiome and resistome of the Chinese populations. *American Society for Microbiology*, *10*(3), 1–22.

Tofani, G. S. S., Leigh, S.-J., Gheorghe, C. E., Bastiaanssen, T. F. S., Wilmes, L., Sen, P., Clarke, G., & Cryan, J. F. (2024). Gut microbiota regulates stress responsivity via the circadian system. *Cell Metabolism*, *37*(1), 138-153.e5. https://doi.org/10.1016/j.cmet.2024.10.003

Valdes, A. M., Walter, J., Segal, E., & Spector, T. D. (2018). Role of the gut microbiota in nutrition and health. *BMJ*, *361*, 36–44. https://doi.org/10.1136/bmj.k2179

Wagner, K. H., & Brath, H. (2012). A global view on the development of non communicable diseases. *Preventive Medicine*, *54*(SUPPL.), S38–S41. https://doi.org/10.1016/j.ypmed.2011.11.012

Wu, W.-L., Adame, M. D., Liou, C.-W., Barlow, J. T., Lai, T.-T., Sharon, G., Schretter, C. E., Needham, B. D., Wang, M. I., Tang, W., Ousey, J., Lin, Y.-Y., Yao, T.-H., Abdel-Haq, R., Beadle, K., Gradinaru, V., Ismagilov, R. F., & Mazmanian, S. K. (2021). Microbiota regulate social behaviour via stress response neurons in the brain. *Physiology & Behavior*, *595*(7867), 409–414. https://doi.org/10.1002/hep.30150.Ductular

Xu, C., Lee, S. K., Zhang, D., & Frenette, P. S. (2020). The gut microbiome regulates psychological-stress-induced inflammation. *Immunity*, *53*(2), 417-428.e4. https://doi.org/10.1016/j.immuni.2020.06.025

Xu, J., Becker, A. A. M. J., Luo, Y., Zhang, W., Ge, B., Leng, C., Wang, G., Ding, L., Wang, J., Fu, X., & Janssens, G. P. J. (2021). The fecal microbiota of dogs switching to a raw diet only partially converges to that of wolves. *Frontiers in Microbiology*, *12*(September). https://doi.org/10.3389/fmicb.2021.701439

Yang, Y. C., Boen, C., Gerken, K., Li, T., Schorpp, K., & Harris, K. M. (2016). Social relationships and physiological determinants of longevity across the human life span. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(3), 578–583. https://doi.org/10.1073/pnas.1511085112

Yarlagadda, K., Zachwieja, A. J., De Flamingh, A., Phungviwatnikul, T., Rivera-Colon, A. G., Roseman, C., Shackelford, L., Swanson, K. S., & Malhi, R. S. (2022). Geographically diverse canid sampling provides novel insights into pre-industrial microbiomes. *Proceedings of the Royal Society B: Biological Sciences*, *289*(1974). https://doi.org/10.1098/rspb.2022.0052

Yegorov, Y. E., Poznyak, A. V., Nikiforov, N. G., Sobenin, I. A., & Orekhov, A. N. (2020). The link between chronic stress and accelerated aging. *Biomedicines*, *8*(8), 1–14. https://doi.org/10.3390/BIOMEDICINES8070198

Chapter 7

Conclusion

Dissertation summary

This dissertation investigates the biological and behavioral adaptations that have enabled domestic dogs to live successfully alongside humans across a wide range of environments. Specifically, it explores how changes in stress physiology, cognition, diet, and the gut microbiome have contributed to dogs' flexibility and success. By examining these adaptations, this work aims to deepen our understanding of the processes of domestication and to highlight the complex ways in which dogs have co-evolved with human societies.

The domestic dog is a remarkable example of an animal that has successfully adapted to diverse lifestyles across human societies worldwide. Dogs have lived among humans for tens of thousands of years (Freedman & Wayne, 2017; Janssens et al., 2018), spreading to most human societies on every inhabited continent (Balme et al., 2018; Bergström et al., 2020; Lupo, 2017; Perri et al., 2021) and fulfilling diverse roles (Chambers et al., 2020; Coppinger & Coppinger, 2000; Hall et al., 2021; Lupo, 2019; Perri, 2020). Several adaptations have likely contributed to dogs' ability to live and cooperate with humans under such a wide range of conditions. A reduced stress response appears to have been critical for domestication (Zeder, 2012). Among the genes that are highly differentiated between dogs and wolves, genes involved in the fight-or-flight response are particularly overrepresented (Cagan & Blass, 2016). Compared to wolves, dogs have much lower fear of novelty and humans (Salomons et al., 2021). Reduced fear of humans is the most widely shared trait of domestic animals compared to their wild relatives (Sánchez-Villagra et al., 2016). Experimental domestication studies, such as the long-term selection of foxes for tameness, show that reduced fear of humans is linked to the pleiotropic emergence of various dog-like traits, with alterations to the hypothalamic-pituitary-adrenal (HPA) axis likely serving as a main target of selection (Trut et al., 2009; Wilkins et al., 2014). Cognitive changes, particularly in social cognition, also appear to be a key part of domestication that has endowed dogs with exceptional versatility in human interactions. Compared to wolves, dogs are better at comprehending human gestures and are more likely to look to humans when faced with unsolvable problems (Hare et al., 2002; Miklósi et al., 2003; Salomons et al., 2021). Furthermore, cognitive variation within dogs, especially in the social domain, predicts which dogs will be more successful as working dogs (MacLean & Hare, 2018).

Beyond social adaptations to living with humans, domestication and the global spread of dogs also required dietary adaptation. Dogs commonly consume diets similar to those of the human population they live among (Guiry, 2012, 2013), and they have undergone convergent evolution with humans in terms of genes such as amylase, reflecting adaptation to starch-rich diets (Axelsson et al., 2013). The microbiome may be one mechanism by which dogs can adapt to these new diets. Prior to the evolution of their own amylase genes, Bronze Age dogs in Italy had gut microbiomes that were enriched in amylase genes compared to the microbiomes of modern dogs (Rampelli et al., 2021). Shifts in the gut microbiomes of domesticated species mirror changes seen in human microbiomes across our evolutionary history and recent industrialization (Reese et al., 2021). Diet swap experiments indicate that dog and wolf microbiome differences seem to be in part related to diet (Reese et al., 2021; Xu et al., 2021). Additionally, comparisons of dog gut microbiomes around the world indicate an adaptive role for the microbiome, with greater diversity of *Lactobacillus* associated with regions and households whose dogs consume more dairy products (Yarlagadda et al., 2022). Understanding these biological and ecological adaptations not only sheds light on the history of domestication, but also informs broader questions about co-evolution, adaptation, and resilience in changing environments.

In Chapter 2 of this dissertation, I explored the important role that studies of dogs can play in anthropology research. Given their global distribution and remarkable adaptability, understanding how domestic dogs became so well-suited to living among humans is a critical area of study. I argue that dogs offer valuable opportunities for contributions across multiple subfields of anthropology. Research on dogs can enhance archaeological studies of past populations, inform cultural anthropological investigations of human diversity, illuminate how humans impact the evolution of other species, and contribute to studies of human communication, cooperation, evolutionary adaptation, and health variation. In analyses that involve the destructive sampling of archaeological remains (e.g., isotopic or genetic analyses), dogs may serve as useful proxies for humans. Specifically, sampling dog remains may be practically and ethically more suitable than sampling human remains (Guiry, 2012, 2013). Dogs have also experienced convergent evolution with humans in several domains, including dietary adaptations (Axelsson et al., 2013), high altitude tolerance (Wang et al., 2014), parasite resistance (Liu et al., 2018), and aspects of their social cognition (Hare, 2017). Furthermore, because dogs share many environmental exposures with humans, experience similar causes of death, and exhibit compressed aging trajectories, they offer a promising model for studying chronic health and aging (Hoffman et al., 2018). From an ethical standpoint, I propose that researchers working with pet dogs should not only follow established animal research guidelines (National Research Council, 2011), but should also design studies in line with ethical standards developed for research involving human populations with limited autonomy (National Commission for the Protection of Human Subjects of Biomedical and Behavioral Research, 1979). I also explicitly lay the groundwork for the subsequent chapters by highlighting areas where dog research can make a contribution.

In Chapter 3, I examine the relationship between dog cognition and behavior by comparing individual variation in cognitive tasks to survey responses from owners in a large citizen science dataset. Through the Dognition project, thousands of dog owners conducted a battery of cognitive tasks with their dogs as well as answered survey questions about their behavior. I identified survey questions that were likely to be associated with particular cognitive tasks, based on possible interpretations of the traits being measured. Performance on gesture-comprehension tasks correlated with owner reports of dogs' real-world communication with humans, while performance on memory tasks correlated with ratings of dogs' memory abilities across various contexts. Additionally, dogs who were more likely to steal food when unobserved in a cognitive task were also rated by their owners as more likely to steal food in everyday life. Two reasoning tasks show only limited associations with questions about the dogs' reasoning in the real world, and an eye contact task in which a treat is held near the eye appeared to capture elements of both human interest and food motivation. These findings provide important context for interpreting other studies that use similar tasks to draw inferences about differences between dogs and wolves as well as variation with dogs. For instance, while some authors interpret dogs' higher rates of following human gestures compared to wolves as evidence of an evolved propensity for human communication (Salomons et al., 2021), others suggest it simply reflects greater interest in humans (Hansen Wheat et al., 2023). The results from this chapter, which show that gesture comprehension relates strongly to communicative ability across a broad range of contexts, support the former interpretation. Additionally, previous work has shown that performance on tasks such as gesture comprehension and memory is associated with the success of military detection dogs, although the underlying reasons remained unclear (MacLean & Hare, 2018). My findings indicate that variation in dogs' communication and memory in various contexts correlates with performance on these tasks, which suggests that dogs may be utilizing their communicative abilities and memory to be more successfully trained at these tasks.

In Chapter 4, I continued to examine the relationship between dogs' cognition and real-world behavior. I conducted five cognitive tasks with a sample of dogs, observed their behavior through focal follows in a dog park, and surveyed owners about their dogs' personalities. While the citizen science approach described in the previous chapter offered the advantage of large sample sizes and greater statistical power, it carried the risk of bias and reduced rigor, as tasks were performed by untrained participants in uncontrolled home environments. Additionally, certain methods, such as standardized ethological observations, were not feasible in that context. In contrast, the study described in this chapter allowed me to directly administer the cognitive tasks, observe dogs in a naturalistic setting during a 30-minute dog park observation, and include cognitive tasks not available in the Dognition dataset. Overall, I did not find significant evidence of the predicted relationships between cognitive tasks and observed behavior or owner survey results. However, a few associations emerged contrary to my predictions. For instance, dogs rated as more communicative made less eye contact on a task they could not solve without human help, and dogs rated as having higher training focus were more likely to run into a transparent cylinder on their way to get a treat instead of taking a detour. One possible interpretation is that the cylinder task measures not only self-control but also food motivation: more highly food motivated dogs may be more likely both to touch the cylinder and to be highly trainable. I also observed a decreasing likelihood of dogs touching the cylinder across the ten trials, highlighting the need for researchers to account for learning effects when using this task. Furthermore, I found that dogs performed better on the version of the pointing task in which the human's arm was fully extended compared to two more challenging variations. This suggests that the more difficult versions may be preferable for studying individual variation within dog populations in order to avoid ceiling effects.

In Chapter 5, I examined the relationship between physiological measures of stress, specifically salivary and hair cortisol, and behavioral observations, a temperament task, and owner surveys. I collected salivary cortisol from dogs before and after a 30-minute focal follow in a dog park. Because salivary cortisol reflects short-term HPA axis activity, whereas hair cortisol captures average levels over several months, I collected both measures to assess acute and chronic stress, respectively. In addition, I administered two previously validated surveys and a temperament task involving a sudden opening of an umbrella to assess dogs' general tendencies toward fear and stress. The cortisol assays showed high reliability: duplicate measures of salivary cortisol were very consistent, and pre- and post-observation salivary cortisol levels were moderately strongly correlated, indicating that the assays reliably measured cortisol levels. However, I generally did not find significant associations between either salivary or hair cortisol and the other measures of stress, including no significant correlation between the two cortisol measures themselves. The one notable exception was that dogs whose salivary cortisol remained above a cut-off value of 0.4 µg/dL at both time points exhibited higher rates of stress-related behaviors, such as tucking their tails, during the dog park observation. These findings align with other recent studies that have reported limited associations between salivary cortisol and behavioral measures of stress (Ferrans et al., in press; Hughes-Duvall, 2024) or have found significant associations using the same cut-off level (McPeake et al., 2021). Taken together, these results suggest that although salivary cortisol is widely used as a biomarker of stress in dogs, its utility may be limited to identifying acute stress through very high levels rather than serving as a continuous quantitative measurement of stress. Future studies should consider incorporating serum cortisol or other biomarkers to more comprehensively assess canine stress responses.

In Chapter 6, I explore how the oral and gut microbiomes of dogs relate to their demographic and behavioral characteristics, and I compare these dogs to dogs and wolves from published datasets to assess the relevance of the microbiome to dog domestication. The ways in which stress, social relationships, and diet relate to the microbiome are an expanding area of interest because they are all factors that can affect chronic health outcomes. They are also major factors that differ between dogs and wolves. I found limited evidence that the microbiome is associated with stress or social variables, specifically detecting differences in oral microbiome composition depending on whether dogs lived with other dogs, and in gut microbiome composition based on dogs' responses to a temperament task. However, the clearest associations involved the effect of age: older dogs exhibited greater bacterial diversity in their oral microbiomes, and both community composition and the relative abundance of specific microbes shifted along an age gradient. Given that noncommunicable diseases are strongly associated with aging, are more prevalent in industrialized societies, and are often causally linked to the microbiome, the observed relationship between age and the oral microbiome in dogs warrants further investigation. Future research should examine age-related microbiome changes across different dog populations and their potential connections to chronic health conditions. When comparing the microbiomes of the dogs I sampled to those of previously studied dogs and wolves, I found strong effects of host species, but also notable study-specific effects, highlighting both the reality of a domestication-driven microbiome shift and the challenges of cross-study comparisons due to population or methodological differences. One of the most striking differences was the higher prevalence of *Lactobacillus* in dog guts as compared to wolf guts, which may reflect an adaptation that facilitates the consumption of dairy products in human societies where dairy is a common food source.

To conclude, this dissertation begins by arguing that scientific research on dogs has underutilized potential for advancing anthropological inquiry. I then analyze a large citizen science dataset, comparing dog cognition to owner-reported behavior, and find evidence that performance on various cognitive tasks is associated with related real-world behaviors. Building on this, I compare a set of cognitive tasks to dogs' behavior during dog park observations and to owner surveys on dog personality, finding that a task designed to measure self-control may instead reflect aspects of dogs' motivation. In the same sample, I investigate correlations between salivary and hair cortisol and behavioral indicators of stress, finding limited support for salivary cortisol as a marker of acute stress but not as a continuous stress biomarker. Finally, I examine factors influencing variation in the oral and gut microbiomes of dogs and identify an age-related gradient in the oral microbiome composition of non-geriatric adult dogs.

Significance

This dissertation makes several contributions to both anthropology and dog research. Its primary focus is the validation of measures widely used in the study of dogs, humans, and other animals, providing a practical contribution by helping to contextualize and interpret findings reliant on these tools. Because research on dog domestication frequently utilizes the measures examined here, my findings offer important context for understanding broader conclusions about the domestication process. The same applies to studies of variation among dogs and the factors that drive such variation. Finally, this dissertation advocates for the broader value of dogs as a model for advancing our understanding of humans and highlights several key areas where future research may be particularly fruitful.

Through my efforts to validate measures of dog cognition and stress, my research contributes to the interpretation of these measures in a broader body of work. In Chapter 2, I note that the cognitive similarities of dogs and humans have been used to propose that dogs are a useful evolutionary model for human cognition, and therefore research is needed that clarifies the traits being measured by dog cognition tasks. My findings in Chapter 3 suggest that dog cognition tasks like pointing comprehension, memory, and the tendency to steal food when unobserved correlate with real-world observations of relevant behaviors in dogs, as do tasks measuring reasoning and smell, albeit to a more limited extent. Several of these tasks, especially the pointing task, have been widely used and discussed in the context of understanding dog cognition (Hare et al., 2002; ManyDogs Project, Espinosa, et al., 2023; Salomons et al., 2021; Udell et al., 2008). In other instances, my findings reveal more ambiguity or nuance in the interpretation of particular measures. For example, Chapter 3 demonstrates that measurements of dogs' eye contact with humans that also include a treat near the eye may also be measuring dogs' interest in food, so this methodological nuance should be considered in the interpretation of this task. In Chapter 4, I found that dogs that touched a clear cylinder more frequently before acquiring food were rated by owners as lower in training focus, contrary to my expectations. This task has traditionally been interpreted in the literature as measuring self-control, which would be expected to be correlated with training focus. Therefore, interpretations of this task should be made with caution, keeping in mind that food motivation may also be an aspect of individual variation on this task. Finally, Chapter 5 examines cortisol, a widely used biological proxy for stress in dogs and other species, but only finds a correlation of salivary cortisol with behavioral measures of stress when levels above a 0.4 µg/dL threshold are compared to behaviors indicative of acute stress in between the collection of two samples. Given these findings, future research using salivary cortisol should approach its interpretation with caution, especially when considering lower values. Focusing on significantly elevated cortisol levels above this threshold may provide more reliable insights into stress in dogs than treating it continuously. Finding ways to measure stress in dogs is particularly important, as noted in Chapter 2, because this can inform our understanding of how domestication has changed animals' stress response and of how chronic stress affects health.

The research in this dissertation helps contextualize the broader literature on dog domestication and how dogs differ from gray wolves. Previous studies have shown that dogs outperform wolves at comprehending human gestures, but the interpretation of this finding has been disputed (Hansen Wheat et al., 2023; Hare et al., 2002; Salomons et al., 2021). In Chapter 3, I found that dogs' performance on a pointing task correlates with ratings of their communicative ability in a variety of contexts. This supports interpretations suggesting that dogs have evolved social cognition to facilitate communication with humans (Salomons et al., 2021) over interpretations that this merely reflects dogs' greater interest in humans (Hansen Wheat et al., 2023). In addition, wolves show greater fear of novelty than dogs do (Salomons et al., 2021). The HPA axis, which coordinates the stress response and regulates cortisol release, differs between domesticated and control foxes (Trut et al., 2009) and is thought to be involved in the differences in stress response between wild and domesticated species (Wilkins et al., 2014). In Chapter 5, I did not find a relationship between cortisol and behavioral measures of chronic stress in dogs, suggesting that comparisons of cortisol between dogs and wolves may not be the most productive way to understand differences in chronic stress experiences. The chronic glucocorticoid response in prey animals to predator presence varies depending on factors such as lifespan and the cyclical nature of predator risk, suggesting that the relationship between the HPA axis and stress may evolve to adapt to different ecological conditions (Boonstra, 2013). A more holistic approach to studying stress that incorporates multiple biomarkers and behavioral measures may be the most fruitful way to study how the stress response differs between dogs and wolves. Finally, comparisons of dog and wolf microbiomes have gained attention in recent years (Podar et al., 2024; Reese et al., 2021; Xu et al., 2021). In Chapter 6, I analyzed the oral and gut microbiomes of dogs I sampled and compared them with previously published microbiome data from dogs and wolves. I found clear differences between host species even after controlling for study variables. These findings reinforce evidence from other studies that there are distinct microbial taxa that differ between dogs and wolves. The differences in microbial composition may reflect adaptations to the diets of dogs, which are more similar to those of the humans they live with, such as the higher prevalence of *Lactobacillus* in dogs, possibly as an adaptation to a diet that includes dairy products.

In addition to contextualizing research on dog-wolf differences, this dissertation also provides insights into variation within dogs. Cognitive tasks such as gesture comprehension and short-term memory have been found to predict the success of military detection dogs (MacLean & Hare, 2018), and cognition is thought to be critical for the success of working dogs (Bray et al., 2021; Hare & Ferrans, 2021). Chapter 3 demonstrates that these cognitive tasks correspond to real-world measures of communication and memory, which helps contextualize why these associations exist in working dogs. Among dogs, those who are more fearful of strangers have significantly shorter lifespans (Dreschel, 2010). While cortisol is often used as the go-to biomarker for measuring stress in dogs, Chapter 5 adds to the growing literature suggesting its limitations, underscoring the need for alternative biomarkers (Ferrans et al., in press; Hughes-Duvall, 2024). In Chapter 6, I demonstrate that the oral microbiome of pet dogs differs as a function of age. This suggests that research on dog microbiomes ought to take age-related effects into consideration in their analyses and interpretations. The field of dog microbiome research is rapidly expanding, and further investigations into how dogs' microbiomes evolve with age and how these changes may be linked to an increased risk of disease as dogs age hold considerable promise.

This dissertation underscores the importance and potential of dogs as a model for understanding human biology and behavior. In Chapter 2, I argue that anthropologists can strengthen many areas of their research by incorporating the study of dogs, whether in understanding human evolution, past and present cultural diversity, or human health. While dogs have already garnered attention in specific anthropological contexts, such as their use as proxies for humans in stable isotope analysis (Guiry, 2012, 2013) or as a model for the evolution of human social cognition and temperament (Hare, 2017; MacLean et al., 2017; Theofanopoulou et al., 2017), that chapter synthesizes a broad range of ways in which dogs can contribute to anthropology. The findings of Chapters 3 and 4, which examine the correlates of cognitive tasks used to study dogs, will be valuable for research on cognitive similarities between dogs and humans. In fact, humans are in some ways more cognitively similar to dogs than to chimpanzees (Hare et al., 2002; MacLean et al., 2017). Chapters 5 and 6 extend this application of dog research to human health by focusing on stress and the microbiome. Chronic stress has been linked to negative health outcomes in both humans (O’Connor et al., 2021) and dogs (Dreschel, 2010), but the mechanisms underlying this remain poorly understood. Similarly, the microbiome, which mediates a wide range of health conditions, is a relatively new area of research. However, as sequencing costs for microbiome analyses have decreased, there is an increasing body of dog microbiome data available that has not yet been fully explored. The environmental similarities between dogs and humans enable research on how environmental factors impact health, and dogs’ shorter lifespans allow for quicker gathering of data on chronic health outcomes. As such, the study of stress and the microbiome in dogs presents a promising model for understanding long-term health, and further research in these areas could yield valuable insights for human health.

In addition to contributing to academic knowledge, my research has also engaged the public in science. Over 50 people in the State College, Pennsylvania, community directly participated in my research, learning about the types of questions researchers are interested in and witnessing firsthand how to study dog cognition. Beyond the participants, many other visitors to Tudek Dog Park became familiar with my research when they saw me observing dogs and took the opportunity to discuss the project with me. It is my hope that these interactions fostered a greater appreciation for the scientific process and demonstrated how research is connected to topics people care about, such as their pets. One particular anecdote from my research highlights the educational impact I hoped to achieve. After concluding data collection with his dog, one participant suggested that his dog was likely choosing the correct cup not because of the pointing gesture but because the dog could smell where the treat was hidden. While this possibility has been explored in other studies of dog pointing comprehension and was not found to significantly influence dogs’ choices (Bray et al., 2020; Hare et al., 2002), instead of dismissing his hypothesis, I invited the participant to test it. We set up the testing area again, performed several trials where the treat was hidden under a cup without any gesture, and the participant saw for himself that his dog performed at chance level in this condition, in contrast to the dog’s accurate performance when the pointing gesture was present. I believe that the most important takeaway from science education is an understanding of how the scientific method works: generating predictions about the world and testing them empirically. I hope that through their involvement in my research, participants gained a deeper appreciation of this principle.

Challenges and limitations

There are several limitations of this dissertation that should be considered in the interpretation of its results. Chapter 3 consists of an analysis of a large citizen science dataset, whereas Chapters 4 through 6 are analyses of a sample of 56 dogs I personally sampled. Each of these data sources has its own strengths and limitations. In citizen science, a lack of oversight and limited ability to train data collectors are a limitation of the quality of the data. Although Dognition participants read instructions and watch a video about how to perform the tasks, there may still be biases or inaccuracies in how they carry out the instructions. Fortunately, a past analysis of this dataset found that results between Dognition and published analyses of the same tasks were broadly comparable, and the use of the redo button in Dognition did not show evidence of use by participants to manipulate the results (Stewart et al., 2015). Despite these findings, having a trained experimenter consistently collect the data, as in the subsequent chapters, is an advantage over the citizen science approach of Chapter 3. On the other hand, the sample I collected has its own drawbacks compared to the Dognition sample. A sample size in the dozens rather than in the thousands has substantially lower statistical power to detect associations and to control for possible confounds such as demographic factors. Additionally, unlike in Dognition where the tests are conducted in the dogs' home by the owners, the dogs I sampled were outside of their homes and interacting with an unfamiliar person. If the dogs were nervous, this could have affected salivary cortisol levels or cognitive task performance. Another limitation of the dog park observations is that they are affected not just by the behavior of the focal dog but also by that of the other dogs in the park. The time dogs spent near other individuals and the behaviors they exhibited (such as fear or play signals) were partially dependent on the interactions with the other dogs and humans, making these observations difficult to interpret reliably.

The sample size limitation mentioned above is one of the most prominent limitations of this dissertation. While the Dognition dataset analyzed in Chapter 3 had very large sample sizes and robust statistical power, the smaller sample sizes of my subsequent chapters limit my ability to interpret the results, especially the null findings. I cannot conclude that these null results indicate a lack of an effect, as there may be an effect that is simply too small in magnitude to be found in 56 or fewer dogs. The power analyses in Chapters 4 and 5 suggest that this sample size may be sufficient for strong to moderately strong relationships, especially when repeated measures are used from dogs, but that weak relationships would be difficult to detect without a large sample. Based on the findings from Chapter 3, which showed a correlation between dog cognition and behavior, it appears that this relationship exists but may be too weak to detect in my smaller sample. This research does, however, lay the groundwork for future research to expand on these findings by conducting similar studies with larger populations of dogs, allowing for more precise comparisons across different samples. Additionally, it will also be possible for future projects to expand on my microbiome analyses by sequencing the remaining samples. In Chapter 6, I analyzed the sequences from the oral microbiomes of 43 dogs and the gut microbiomes of 15 dogs I sampled, but there are 34 additional fecal samples that I have not yet been able to sequence due to logistical constraints. Sequencing these additional samples would increase the sample size and provide the opportunity to examine whether there is an age-related effect in the gut microbiome, assess whether any previously predicted associations are detected, and determine if the relationship between gut microbiome beta diversity and the temperament task holds with a larger sample.

Related to the sample size issue, demographic differences are harder to account for in small samples such as the dogs I sampled in State College. Factors like sex, age, and breed can be associated with variables of interest and structure results in unexpected ways. While I collected demographic information about all the dogs, it is more challenging to control for the effects of these in a small sample, especially for breed, where breeds may be represented by only one or two dogs in the sample. The nature of the questions being asked in this dissertation make these factors relatively less important than they may be in some other studies. As the goal is to validate cognitive tasks and measures of stress rather than to understand why they vary, this means that the existence of sex, age, or breed differences are not of paramount importance. For example, if a sex difference in fearfulness were present, it would be expected that stress behaviors and cortisol would show similar relationships within sexes and overall, even if average scores differed between sexes. However, issues arise when demographic variables cause spurious relationships rather than being directly related to the trait being measured. For example, a sex difference in cortisol could arise from factors unrelated to stress, which could result in apparent correlations between sex and stress behaviors that are not truly causal (or conversely, fail to show a relationship when one exists). Fortunately, large datasets like Dognition suggest that demographic variables may not have a substantial impact on some of the measures studied. For instance, a study with a sample size in the thousands only identified sex differences in a few tasks, and these tasks were not ones I conducted on my sample of Pennsylvania dogs (Watowich et al., 2020). Additionally, while there is evidence for age-related memory decline in geriatric dogs (Watowich et al., 2020), my sample had few dogs that were approaching old age. Breed differences in cognition do exist, such as better memory in breeds with larger brains, but these effects are small in magnitude relative to variation within breeds (Horschler et al., 2019).

When generalizing from a sample to a larger population, it is important to know how representative the sample is of the population as a whole. My sample of pet dogs from Pennsylvania is not representative of dogs globally. Much of the scientific research on dogs focuses on North American and European pet dogs, which differ from dogs in many parts of the world in several important ways. For instance, North American and European dogs are more likely to be spayed or neutered and are more likely to be fed commercial dog food. Indeed, most of the dogs in my sample were spayed or neutered, and all the dogs I have dietary information for eat primarily commercial dog food. Even within the population of pet dogs living in Pennsylvania, it should not be assumed that the dogs sampled are representative. Dogs who visit off-leash dog parks may be a self-selecting group, as dog owners may choose not to take more introverted, aggressive, or fearful dogs to the dog park. With this limitation in mind, this dissertation collects a baseline sample from one population of dogs, and the same methods can be used to sample other populations and compare them. Future research could expand to include working dogs, dogs from other countries, or pet dogs that do not attend dog parks, allowing for comparisons of cognition, cortisol levels, and microbiomes across diverse populations.

Implications for future research

Sample size and statistical power in dog research

One major recommendation for future research in dog cognition and behavior, based on my dissertation, is to leverage the statistical power of large sample sizes. Many studies in the field of dog behavior and cognition have sample sizes of several dozen individuals, or sometimes even fewer. For certain questions, small sample sizes may be sufficient. For instance, the earliest study demonstrating a difference in gesture comprehension between dogs and wolves was able to do so with only seven individuals of each species (Hare et al., 2002). Sometimes, even a study of an individual dog can be informative, such as the demonstration that one exceptional dog is capable of learning the names of over a thousand objects (Pilley & Reid, 2011). However, as research increasingly aims to understand the broad variability within the dog population, larger sample sizes become critical. Larger samples increase statistical power, allowing researchers to detect smaller associations that might be missed with smaller samples. Evidence of this can be seen in a comparison of Chapters 3 and 4, which both compared dog cognition tasks to behavioral measures. In Chapter 4, where I worked with a sample of 56 dogs, I was able to find only a few significant associations. In Chapter 5, sample sizes in the thousands allowed me to find large numbers of small but significant relationships between survey questions and cognitive task performance of dogs.

I would urge other dog researchers to make use of power analyses in their work, especially those power analyses conducted a priori. When researchers conduct a power analysis before conducting a study, they ensure that they are allocating resources in an efficient way and conducting studies that are reasonably likely to be successful at detecting effects of a practically meaningful size, should such effects exist (Quach et al., 2022). Post hoc power analyses to interpret the results of past analyses are common in some fields, but they have been criticized as conceptually flawed, although with the caveat that something can be conceptually flawed yet still useful if interpreted with caution (Quach et al., 2022). A common mistake in post hoc power analyses is to use the sample effect size to represent the population effect size in the calculations, a practice that is known to produce unreliable estimates of statistical power (Quach et al., 2022; Zhang et al., 2019). My suggestion to other dog researchers, which I will implement in my own research going forward, is to conduct power analyses prior to beginning work on a study and to report these results in their research, especially when a statistically significant effect is not detected. This can help with the interpretation of null results while avoiding some of the common pitfalls associated with post hoc power analyses.

Fortunately for researchers, there are a growing number of datasets that present the opportunity to study hundreds or thousands of dogs at once. The Dognition dataset I utilized in Chapter 3 has citizen science data from thousands of dogs on ten different cognitive tasks. Other publications have used this dataset to study the relationship between different cognitive domains of dogs (Stewart et al., 2015), breed differences (Gnanadesikan et al., 2020; Horschler et al., 2019), and age-related cognitive decline (Watowich et al., 2020). Much remains to be gleaned from the Dognition data. As I note in Chapter 3, the survey questions provide a more multifaceted characterization of dogs' memory than a simple short-term memory task, so research on dog aging can use this dataset to look differences in age-related decline in fluid or crystallized memory in dogs. Beyond that, the survey provides a broader window into dogs' behavior than just what can be measured by the cognitive tasks, so the relationship of the survey questions to characteristics like age and breed should be explored. In addition to the main ten cognitive tasks explored by Chapter 3 and various published papers, there are also an additional twelve tasks that were added later to Dognition as a paid add-on. These data have not been explored, but they represent sample sizes of hundreds of dogs and can be used to study the relationship of these tasks to each other and to the ten main tasks. The Dognition data analyzed in this dissertation represent the participants of Dognition through April 2016, but the website remains active at present and has been accumulating new data in the meantime. Not only does this give larger sample sizes, but it also presents an interesting opportunity to study the effects on dogs of a major environmental shift: the COVID-19 pandemic. As large numbers of people began to work from home starting in March 2020, this created a different environment for dogs with less time spent unattended. A comparison of the cognition and behavior of dogs who grew up during this time to those who grew up beforehand could serve as a natural experiment that shows the effects of different rearing patterns.

In addition to citizen science initiatives like Dognition, there are several large-scale collaborative efforts focused on dog cognition, health, and genetics. The ManyDogs Project arose in recent years as a collaboration between various dog cognition laboratories, inspired by and modelled after similar projects like ManyBabies and ManyPrimates (ManyDogs Project, Alberghina, et al., 2023). This project has the stated goal of replicating important findings, addressing inter-laboratory biases, and assembling the large sample sizes needed to answer questions that would be hard for one laboratory to answer alone (ManyDogs Project, Alberghina, et al., 2023). Already this consortium has published a study comparing 455 dogs on two versions of a gesture comprehension task (ManyDogs Project, Espinosa, et al., 2023). Beyond dog cognition, there are also large-scale collaborative projects focused on dog health and genetics. The Dog 10K Project has the goal of sequencing and publishing the genomes of 10,000 canids, including a variety of breeds of dogs, village dogs from around the world, and related canids like wolves and coyotes (Ostrander et al., 2019). As of 2023, they have around 2,000 genomes freely available (Meadows et al., 2023). The Golden Retriever Lifetime Study collected detailed data about 3,000 Golden Retrievers across their lifespans (Guy et al., 2015). An ongoing project called the Dog Aging Project is collecting longitudinal data from thousands of dogs from pure and mixed breeds, including owner surveys, veterinary records, genomes, metabolomes, and microbiomes. Datasets such as these will give researchers high statistical power to answer a wide variety of questions related to dogs' cognition, behavior, and health. I would particularly recommend using such datasets to explore how stress and the microbiome are linked to longevity and chronic health conditions in dogs.

Selection of particular measures

The findings of this dissertation offer several key considerations for dog researchers in their study design, as well as in the selection of specific measures and analyses. In Chapter 6, my analyses detected significant effects of sequencing batch on the oral microbiome as well as significant differences between samples from published studies and my own. This underscores the importance of considering contamination and methodological differences in studies of the microbiome, especially when comparing across labs. My Chapter 5 findings, combined with those of other recent studies (McPeake et al., 2021), suggest that salivary cortisol may be more effective as a measure of acute stress when a threshold of 0.4 μg/dL is used to indicate stress, rather than when cortisol concentration is treated as a continuous fine-grained measure. However, the overall lack of relationship between salivary and hair cortisol with behavioral measures of stress, combined with another recent study's inability to validate dog salivary and serum cortisol samples taken at the same time (Ferrans et al., in press) suggests that biomarkers of stress other than salivary cortisol should be more widely explored as possible alternatives. Serum cortisol remains a more accurate measure than salivary cortisol, although its collection is more practically difficult (Ferrans et al., in press). Other measures that should be considered are salivary α-amylase, which has been found to change in dogs in response to stress when salivary cortisol did not (Hughes-Duvall, 2024), or oxytocin, which may serve a role as coordinating an anti-stress response (Roney, 2016). In Chapter 4, I observed a learning effect in the inhibitory control cylinder task, suggesting that the number of trials should be carefully considered in analyses of this task. Additionally, this task may also reflect the food motivation of dogs, so its results should be interpreted with caution. Future research should continue to explore the correlates of dogs' performance on this task. My findings also suggest that the cross-body pointing task may have some advantages over the extended arm pointing task when looking at individual differences within dogs, as the success rate is lower so there is less of a ceiling effect. In Chapter 3, I found that a task intended to measure dogs' eye contact with humans, which also incorporated a treat held near the eye, appeared to assess both dogs' tendency to make eye contact and their interest in food. This implies that future research on dog-human eye contact should avoid using food rewards to minimize confounding interpretations of this task. Finally, the significant correlations of dog cognition tasks with survey questions in that chapter demonstrates that surveys can also be an effective tool for studying dog cognition. Since surveys are easier to collect in large sample sizes compared to cognitive testing batteries, large-scale studies can use surveys as an alternative method to assess dog cognition.

Opportunities for an anthropological approach to dog research

There are numerous opportunities for future research using companion dogs to explore the factors affecting human health. As dogs live among humans, they experience similar lifestyle variations, making them a valuable model for understanding shared health determinants. Dogs and humans both range from sedentary to highly active, and both species share variations in diet from highly processed foods to greater proportions of raw ingredients. They both experience low to high levels of stress, social interactions, and healthcare access and are exposed to many of the same chemicals, microbes, and climates. With a few exceptions, the causes of death in American dogs and humans occur at similar rates with similar age trajectories and comorbidities (Hoffman et al., 2018). Longitudinal studies of dog health provide opportunities to test hypotheses about how environmental factors affect health as well as to conduct clinical trials of interventions (Kaeberlein et al., 2016). Several exciting opportunities arise from leveraging such datasets to gain insights into both dog and human health. Comparisons of the geographic patterns of particular health conditions in dogs and in humans can point towards possible environmental factors that are driving them. The long-term health effects of chronic stress are particularly worth exploring, as past retrospective research has found that dogs with greater fear of strangers have shorter lives (Dreschel, 2010). Future longitudinal research can track temporal patterns in dogs' stress to see how the timing and duration of stress affects dogs' lifespans. Research in humans experiencing social isolation and loneliness has found a gene expression pattern called the conserved transcriptional response to adversity (CRTA), which includes upregulation of antibacterial immune responses and downregulation of antiviral immune responses (Cole et al., 2007; O'Connor et al., 2021). Experimental manipulation of captive macaques' social status to a lower rank has caused similar gene expression patterns (Snyder-Mackler et al., 2016). It would be valuable for future research to investigate whether this same pattern exists in dogs, which could provide further insight into the underlying mechanisms. For example, if the increased antiviral response is an evolutionary adaptation to the anticipation of higher risk of viral transmission due to increased social interactions, it may not be present in dogs if their primary social partners are humans, who are less likely to spread viruses to them than conspecifics. The canine microbiome also represents a critical area for future longitudinal studies on dog health. As demonstrated in Chapter 6, age affects the oral microbiome of dogs. Large datasets will allow researchers to better understand how dogs' microbiomes shift throughout different life stages, from early development to adulthood and into old age. Research comparing microbiome-health condition relationships in dogs and humans will be valuable regardless of whether the patterns align. Similar patterns could help uncover causal mechanisms behind these associations, while contrasting patterns would raise important questions about the underlying differences. Given the rising prevalence of noncommunicable diseases in association with industrialization (Wagner & Brath, 2012), understanding how dogs' microbiomes and health conditions relate to factors such as exercise, diet, and antibiotic use is of particular importance.

I would also like to emphasize the scientific importance of comparing dogs across cultures and contexts. While most research on dogs is conducted in North America or Europe, pet dogs in these areas differ substantially from dogs in much of the world, such as being more likely to be sterilized, eat designated dog food, receive regular veterinary care, and live in a house instead of ranging freely (Koster, 2021). One of the strengths of anthropology is that it characterizes the human experience more broadly than many research fields do by examining the full scope of diverse conditions humans live in. Dog research should do the same. Indeed, as noted in the previous paragraph, dog research has the potential to help us understand the environmental factors leading to noncommunicable diseases in humans. As these diseases are more common in industrialized countries, studies of dogs in non-industrialized settings will be crucial to making sense of these patterns. There was at least one recent study that compared the gut microbiomes of dogs from several countries with varying levels of industrialization (Yarlagadda et al., 2022). There is also a similar ongoing study examining the microbiomes of dogs from across lifestyle and altitude gradients in Nepal, Thailand, the United Arab Emirates, and the United States, which the gut microbiome samples I collected will form a part of (Jha, pers. comm.). Genetic studies of dogs from different parts of the world have found examples of convergent evolution between the dogs and humans of a particular area, such as increased copy number of amylase genes in agricultural societies (Axelsson et al., 2013) introgressed genes for altitude adaptation in Tibet (Wang et al., 2014), and resistance to malaria-like parasites in Africa (Liu et al., 2018). The genetics of village dogs around the world has been relatively unexplored, so future research could see whether dogs have also managed to converge on other localized human genetic adaptations to particular environments, such high-altitude adaptations in the Andes (Julian & Moore, 2019) or Ethiopian Highlands (Scheinfeldt et al., 2012). The latter of these seems particularly likely in light of Ethiopian wolves being genetically adapted to high altitudes (Mooney et al., 2023) and able to hybridize with domestic dogs (Gottelli et al., 1994). The ethnographic record presents opportunities for comparative studies of the role of dogs in different societies. A recent study assembled a database of mentions of dogs in the Human Relations Area Files ethnographies of 144 cultures (Chambers et al., 2020), which can be used to test hypotheses about why human-dog relationships vary around the world. As my Chapter 3 analyses indicate that the number of words a dog knows according to the owner is correlated with the dog's gesture comprehension, it is worth exploring in this database what factors are linked to variation in dogs being called or commanded verbally, such as whether this is related to specific functions like herding or hunting. While the cognitive profiles of military detection dogs and assistance dogs have been studied (Bray et al., 2020; MacLean & Hare, 2018), there has not yet been a comprehensive effort to understand how dogs' cognitive abilities relate to success in more traditional jobs such as hunting, herding, or pulling sleds. These working dog roles have existed for thousands of years (Coppinger & Coppinger, 2000; Guagnin et al., 2018; Pitulko & Kasparov, 2017), and may have exerted unique selective pressures on dog cognition.

It is my hope that this dissertation lays the groundwork for future research into the cognition, stress, and microbiomes of diverse dog populations around the world and in various working contexts. Such studies would provide valuable insights not only into dog biology but also into the shared evolutionary and environmental factors that shape human and canine health.

References

Axelsson, E., Ratnakumar, A., Arendt, M. L., Maqbool, K., Webster, M. T., Perloski, M., Liberg, O., Arnemo, J. M., Hedhammar, Å., & Lindblad-Toh, K. (2013). The genomic signature of dog domestication reveals adaptation to a starch-rich diet. *Nature*, *495*(7441), 360–364. https://doi.org/10.1038/nature11837

Balme, J., O'Connor, S., & Fallon, S. (2018). New dates on dingo bones from Madura Cave provide oldest firm evidence for arrival of the species in Australia. *Scientific Reports*, *8*(1), 4–9. https://doi.org/10.1038/s41598-018-28324-x

Bergström, A., Frantz, L., Schmidt, R., Ersmark, E., Lebrasseur, O., Girdland-Flink, L., Lin, A. T., Storå, J., Sjögren, K.-G., Anthony, D., Antipina, E., Amiri, S., Bar-Oz, G., Bazaliiskii, V. I., Bulatović, J., Brown, D., Carmagnini, A., Davy, T., Fedorov, S., … Skoglund, P. (2020). Origins and genetic legacy of prehistoric dogs. *Science*, *370*(557–564), 1–7.

Boonstra, R. (2013). Reality as the leading cause of stress: rethinking the impact of chronic stress in nature. *Functional Ecology*, *27*(1), 11–23. https://doi.org/10.1111/1365-2435.12008

Bray, E. E., Gruen, M. E., Gnanadesikan, G. E., Horschler, D. J., Levy, K. M., Kennedy, B. S., Hare, B. A., & MacLean, E. L. (2020). Cognitive characteristics of 8-to-10-week-old assistance dog puppies. *Animal Behaviour*, *166*, 193–206. https://doi.org/10.1016/j.anbehav.2020.05.019

Bray, E. E., Otto, C. M., Udell, M. A. R., Hall, N. J., Johnston, A. M., & MacLean, E. L. (2021). Enhancing the selection and performance of working dogs. *Frontiers in Veterinary Science*, *8*(May). https://doi.org/10.3389/fvets.2021.644431

Cagan, A., & Blass, T. (2016). Identification of genomic variants putatively targeted by selection during dog domestication. *BMC Evolutionary Biology*, *16*(1), 1–13. https://doi.org/10.1186/s12862-015-0579-7

Chambers, J., Quinlan, M. B., Evans, A., & Quinlan, R. J. (2020). Dog-human coevolution: cross-cultural analysis of multiple hypotheses. *Journal of Ethnobiology*, *40*(4), 414–433. https://doi.org/10.2993/0278-0771-40.4.414

Cole, S. W., Hawkley, L. C., Arevalo, J. M., Sung, C. Y., Rose, R. M., & Cacioppo, J. T. (2007). Social regulation of gene expression in human leukocytes. *Genome Biology*, *8*(9). https://doi.org/10.1186/gb-2007-8-9-r189

Coppinger, L., & Coppinger, R. (2000). Dogs for herding and guarding livestock. In T. Grandin (Ed.), *Livestock Handling and Transport* (2nd ed., pp. 235–253).

Dreschel, N. A. (2010). The effects of fear and anxiety on health and lifespan in pet dogs. *Applied Animal Behaviour Science*, *125*(3–4), 157–162. https://doi.org/10.1016/j.applanim.2010.04.003

Ferrans, M., Salomons, H., Moore, K., White, P., Hare, B., & Gruen, M. E. (2025). Salivary cortisol is an unreliable correlate of serum cortisol in adult pet dogs and assistance dog puppies. *Scientific Reports*, *15*(1), 1–11.

Freedman, A. H., & Wayne, R. K. (2017). Deciphering the origin of dogs: from fossils to genomes. *Annual Review of Animal Biosciences*, *5*(1), 281–307. https://doi.org/10.1146/annurev-animal-022114-110937

Gnanadesikan, G. E., Hare, B., Snyder-Mackler, N., & MacLean, E. L. (2020). Estimating the heritability of cognitive traits across dog breeds reveals highly heritable inhibitory control and communication factors. *Animal Cognition*.

Gottelli, D., Sillero-Zubiri, C., Applebaum, G. D., Roy, M. S., Girman, D. J., Garcia-Moreno, J., Ostrander, E. A., & Wayne, R. K. (1994). Molecular genetics of the most endangered canid: the Ethiopian wolf Canis simensis. *Molecular Ecology*, *3*(4), 301–312. https://doi.org/10.1111/j.1365-294X.1994.tb00070.x

Guagnin, M., Perri, A. R., & Petraglia, M. D. (2018). Pre-Neolithic evidence for dog-assisted hunting strategies in Arabia. *Journal of Anthropological Archaeology*, *49*(November 2017), 225–236. https://doi.org/10.1016/j.jaa.2017.10.003

Guiry, E. J. (2012). Dogs as analogs in stable isotope-based human paleodietary reconstructions: a review and considerations for future use. *Journal of Archaeological Method and Theory*, *19*(3), 351–376. https://doi.org/10.1007/s10816-011-9118-z

Guiry, E. J. (2013). A canine surrogacy approach to human paleodietary bone chemistry: Past development and future directions. *Archaeological and Anthropological Sciences*, *5*(3), 275–286. https://doi.org/10.1007/s12520-013-0133-8

Guy, M. K., Page, R. L., Jensen, W. A., Olson, P. N., David Haworth, J., Searfoss, E. E., & Brown, D. E. (2015). The Golden Retriever Lifetime Study: establishing an observational cohort study with translational relevance for human health. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *370*(1673). https://doi.org/10.1098/rstb.2014.0230

Hall, N. J., Johnston, A. M., Bray, E. E., Otto, C. M., MacLean, E. L., & Udell, M. A. R. (2021). Working dog training for the twenty-first century. *Frontiers in Veterinary Science*, *8*(July), 1–18. https://doi.org/10.3389/fvets.2021.646022

Hansen Wheat, C., van der Bijl, W., & Wynne, C. D. L. (2023). Rearing condition and willingness to approach a stranger explain differences in point following performance in wolves and dogs. *Learning and Behavior*, *51*(2), 127–130. https://doi.org/10.3758/s13420-022-00544-2

Hare, B. (2017). Survival of the friendliest: Homo sapiens evolved via selection for prosociality. *Annual Review of Psychology*, *68*(1), 155–186. https://doi.org/10.1146/annurev-psych-010416-044201

Hare, B., Brown, M., Williamson, C., & Tomasello, M. (2002). The domestication of social cognition in dogs. *Science*, *298*(5598), 1634–1636. https://doi.org/10.1126/science.1072702

Hare, B., & Ferrans, M. (2021). Is cognition the secret to working dog success? *Animal Cognition*, *24*(2), 231–237. https://doi.org/10.1007/s10071-021-01491-7

Hoffman, J. M., Creevy, K. E., Franks, A., O'Neill, D. G., & Promislow, D. E. L. (2018). The companion dog as a model for human aging and mortality. *Aging Cell*, *17*(3). https://doi.org/10.1111/acel.12737

Horschler, D. J., Hare, B., Call, J., Kaminski, J., Miklósi, Á., & MacLean, E. L. (2019). Absolute brain size predicts dog breed differences in executive function. *Animal Cognition*, *22*(2), 187–198. https://doi.org/10.1007/s10071-018-01234-1

Hughes-Duvall, K. (2024). *Does early life history influence a novel biomarker for stress in dogs and predict their attachment to their owners?*

Janssens, L., Giemsch, L., Schmitz, R., Street, M., Van Dongen, S., & Crombé, P. (2018). A new look at an old dog: Bonn-Oberkassel reconsidered. *Journal of Archaeological Science*, *92*, 126–138. https://doi.org/10.1016/j.jas.2018.01.004

Jha, A. R. (n.d.). *personal communication*.

Julian, C. G., & Moore, L. G. (2019). Human genetic adaptation to high altitude: evidence from the Andes. *Genes*, *10*(2). https://doi.org/10.3390/genes10020150

Kaeberlein, M., Creevy, K. E., & Promislow, D. E. L. (2016). The Dog Aging Project: translational geroscience in companion animals. *Mammalian Genome*, *27*(7–8), 279–288. https://doi.org/10.1007/s00335-016-9638-7.The

Koster, J. (2021). Most Dogs Are Not NATIVE Dogs. *Integrative and Comparative Biology*, *61*(1), 110–116. https://doi.org/10.1093/icb/icab016

Liu, Y.-H., Wang, L., Xu, T., Guo, X., Li, Y., Yin, T.-T., Yang, H.-C., Hu, Y., Adeola, A. C., Sanke, O. J., Otecko, N. O., Wang, M., Ma, Y., Charles, O. S., Sinding, M.-H. S., Gopalakrishnan, S., Samaniego, J. A., Hansen, A. J., Fernandes, C., … Zhang, Y.-P. (2018). Whole-genome sequencing of African dogs provides insights into adaptations against tropical parasites. *Molecular Biology and Evolution*, *35*(2), 287–298. https://doi.org/10.1093/molbev/msx258

Lupo, K. D. (2017). When and where do dogs improve hunting productivity? The empirical record and some implications for early Upper Paleolithic prey acquisition. *Journal of Anthropological Archaeology*, *47*, 139–151. https://doi.org/10.1016/j.jaa.2017.05.003

Lupo, K. D. (2019). Hounds follow those who feed them: What can the ethnographic record of hunter-gatherers reveal about early human-canid partnerships? *Journal of Anthropological Archaeology*, *55*(April), 101081. https://doi.org/10.1016/j.jaa.2019.101081

MacLean, E. L., & Hare, B. (2018). Enhanced selection of assistance and explosive detection dogs using cognitive measures. *Frontiers in Veterinary Science*, *5*(236), 1–14. https://doi.org/10.3389/fvets.2018.00236

MacLean, E. L., Herrmann, E., Suchindran, S., & Hare, B. (2017). Individual differences in cooperative communicative skills are more similar between dogs and humans than chimpanzees. *Animal Behaviour*, *126*, 41–51. https://doi.org/10.1016/j.anbehav.2017.01.005

ManyDogs Project, Alberghina, D., Bray, E. E., Buchsbaum, D., Byosiere, S. E., Espinosa, J., Gnanadesikan, G. E., Guran, C. N. A., Hare, E., Horschler, D. J., Huber, L., Kuhlmeier, V. A., MacLean, E. L., Pelgrim, M. H., Perez, B., Ravid-Schurr, D., Rothkoff, L., Sexton, C. L., Silver, Z. A., & Stevens, J. R. (2023). ManyDogs Project: a big team science approach to investigating canine behavior and cognition. *Comparative Cognition and Behavior Reviews*, *18*, 59–77. https://doi.org/10.3819/CCBR.2023.180004

ManyDogs Project, Espinosa, J., Stevens, J. R., Alberghina, D., Alway, H. E. E., Barela, J. D., Bogese, M., Bray, E. E., Buchsbaum, D., Byosiere, S.-E., Byrne, M. B., Cavalli, C. M., Chaudoir, L. M., Collins-Pisano, C., DeBoer, H. J., Douglas, L. E. L. C., Dror, S., Dzik, M. V., Ferguson, B., … Zylberfuden, S. G. (2023). ManyDogs 1: a multi-lab replication study of dogs' pointing comprehension. *Animal Behavior and Cognition*, *10*(3), 232–286. https://doi.org/10.26451/abc.10.03.03.2023

McPeake, K. J., Collins, L. M., Zulch, H., & Mills, D. S. (2021). Behavioural and physiological correlates of the Canine Frustration Questionnaire. *Animals*, *11*(3346), 1–15.

Meadows, J. R. S., Kidd, J. M., Wang, G. D., Parker, H. G., Schall, P. Z., Bianchi, M., Christmas, M. J., Bougiouri, K., Buckley, R. M., Hitte, C., Nguyen, A. K., Wang, C., Jagannathan, V., Niskanen, J. E., Frantz, L. A. F., Arumilli, M., Hundi, S., Lindblad-Toh, K., Ginja, C., … Ostrander, E. A. (2023). Genome sequencing of 2000 canids by the Dog10K consortium advances the understanding of demography, genome function and architecture. *Genome Biology*, *24*(1). https://doi.org/10.1186/s13059-023-03023-7

Miklósi, Á., Kubinyi, E., Topál, J., Gácsi, M., Virányi, Z., & Csányi, V. (2003). A simple reason for a big difference: Wolves do not look back at humans, but dogs do. *Current Biology*, *13*(13), 763–766. https://doi.org/10.1016/S

Mooney, J. A., Marsden, C. D., Yohannes, A., Wayne, R. K., & Lohmueller, K. E. (2023). Long-term small population size, deleterious variation, and altitude adaptation in the Ethiopian wolf, a severely endangered canid. *Molecular Biology and Evolution*, *40*(1), 1–14. https://doi.org/10.1093/molbev/msac277

National Commission for the Protection of Human Subjects of Biomedical and Behavioral Research. (1979). *The Belmont Report*. https://doi.org/10.1021/bi00780a005

National Research Council. (2011). *Guide for the care and use of laboratory animals* (8th ed.). National Academies Press. https://doi.org/10.17226/12910

O’Connor, D. B., Thayer, J. F., & Vedhara, K. (2021). Stress and health: a review of psychobiological processes. *Annual Review of Psychology*, *72*, 663–688. https://doi.org/10.1146/annurev-psych-062520-122331

Ostrander, E. A., Wang, G. D., Larson, G., Vonholdt, B. M., Davis, B. W., Jagannathan, V., Hitte, C., Wayne, R. K., Zhang, Y. P., André, C., Axelsson, E., Boyko, A., Forman, O., Frantz, L., Karlsson, E., Kidd, J., Leeb, T., Lindblad-Toh, K., Lohi, H., … Zhai, W. (2019). Dog10K: an international sequencing effort to advance studies of canine domestication, phenotypes and health. *National Science Review*, *6*(4), 810–824. https://doi.org/10.1093/nsr/nwz049

Perri, A. R. (2020). Prehistoric dogs as hunting weapons: the advent of animal biotechnology. In B. Berthke & A. Burtt (Eds.), *Dogs: Archaeology of the Human-Canine Connection Beyond Domestication* (pp. 7–44). University Press of Florida.

Perri, A. R., Feuerborn, T. R., Frantz, L. A. F., Larson, G., & Malhi, R. S. (2021). Dog domestication and the dual dispersal of people and dogs into the Americas. *Proceedings of the National Academy of Sciences*, *118*(6), 1–8. https://doi.org/10.1073/pnas.2010083118

Pilley, J. W., & Reid, A. K. (2011). Border collie comprehends object names as verbal referents. *Behavioural Processes*, *86*(2), 184–195. https://doi.org/10.1016/j.beproc.2010.11.007

Pitulko, V. V., & Kasparov, A. K. (2017). Archaeological dogs from the Early Holocene Zhokhov site in the Eastern Siberian Arctic. *Journal of Archaeological Science: Reports*, *13*(May), 491–515. https://doi.org/10.1016/j.jasrep.2017.04.003

Podar, N. A., Carrell, A. A., Cassidy, K. A., Klingeman, D. M., Yang, Z., Stahler, E. A., Smith, D. W., Stahler, D. R., & Podar, M. (2024). From wolves to humans: oral microbiome resistance to transfer across mammalian hosts. *MBio*, *15*(3). https://doi.org/10.1128/mbio.03342-23

Quach, N. E., Yang, K., Chen, R., Tu, J., Xu, M., Tu, X. M., & Zhang, X. (2022). Post-hoc power analysis: a conceptually valid approach for power based on observed study data. *General Psychiatry*, *35*(4), 1–7. https://doi.org/10.1136/gpsych-2022-100764

Rampelli, S., Turroni, S., Debandi, F., Alberdi, A., Schnorr, S. L., Hofman, C. A., Taddia, A., Helg, R., Biagi, E., Brigidi, P., D'Amico, F., Cattani, M., & Candela, M. (2021). The gut microbiome buffers dietary adaptation in Bronze Age domesticated dogs. *IScience*, 135907. https://doi.org/10.1016/j.isci.2021.102816

Reese, A. T., Chadaideh, K. S., Diggins, C. E., Schell, L. D., Beckel, M., Callahan, P., Ryan, R., Thompson, M. E., & Carmody, R. N. (2021). Effects of domestication on the gut microbiota parallel those of human industrialization. *ELife*, *10*, 1–27. https://doi.org/10.7554/eLife.60197

Roney, J. R. (2016). Theoretical frameworks for human behavioral endocrinology. *Hormones and Behavior*, *84*, 97–110. https://doi.org/10.1016/j.yhbeh.2016.06.004

Salomons, H., Smith, K. C. M., Callahan-Beckel, M., Callahan, M., Levy, K., Kennedy, B. S., Bray, E. E., Gnanadesikan, G. E., Horschler, D. J., Gruen, M., Tan, J., White, P., VonHoldt, B. M., MacLean, E. L., & Hare, B. (2021). Cooperative communication with humans evolved to emerge early in domestic dogs. *Current Biology*, *31*(July), 1–8. https://doi.org/10.1016/j.cub.2021.06.051

Sánchez-Villagra, M. R., Geiger, M., & Schneider, R. A. (2016). The taming of the neural crest: A developmental perspective on the origins of morphological covariation in domesticated mammals. *Royal Society Open Science*, *3*(6). https://doi.org/10.1098/rsos.160107

Scheinfeldt, L. B., Soi, S., Thompson, S., Ranciaro, A., Woldemeskel, D., Beggs, W., Lambert, C., Jarvis, J. P., Abate, D., Belay, G., & Tishkoff, S. A. (2012). Genetic adaptation to high altitude in the Ethiopian highlands. *Genome Biology*, *13*(1), R1. https://doi.org/10.1186/gb-2012-13-1-r1

Snyder-Mackler, N., Sanz, J., Kohn, J. N., Brinkworth, J. F., Morrow, S., Shaver, A. O., Grenier, J. C., Pique-Regi, R., Johnson, Z. P., Wilson, M. E., Barreiro, L. B., & Tung, J. (2016). Social status alters immune regulation and response to infection in macaques. *Science*, *354*(6315), 1041–1045. https://doi.org/10.1126/science.aah3580

Stewart, L., MacLean, E. L., Ivy, D., Woods, V., Cohen, E., Rodriguez, K., McIntyre, M., Mukherjee, S., Call, J., Kaminski, J., Miklósi, Á., Wrangham, R. W., & Hare, B. (2015). Citizen science as a new tool in dog cognition research. *PLoS ONE*, *10*(9), 1–16. https://doi.org/10.1371/journal.pone.0135176

Theofanopoulou, C., Gastaldon, S., O’Rourke, T., Samuels, B. D., Messner, A., Martins, P. T., Delogu, F., Alamri, S., & Boeckx, C. (2017). Self-domestication in Homo sapiens: insights from comparative genomics. *PLoS ONE*, *12*(10), 5–7. https://doi.org/10.1371/journal.pone.0185306

Trut, L., Oskina, I., & Kharlamova, A. (2009). Animal evolution during domestication: the domesticated fox as a model. *Bioessays*, *31*(3), 349–360. https://doi.org/10.1038/jid.2014.371

Udell, M. A. R., Dorey, N. R., & Wynne, C. D. L. (2008). Wolves outperform dogs in following human social cues. *Animal Behaviour*, *76*(6), 1767–1773. https://doi.org/10.1016/j.anbehav.2008.07.028

Wagner, K. H., & Brath, H. (2012). A global view on the development of non communicable diseases. *Preventive Medicine*, *54*(SUPPL.), S38–S41. https://doi.org/10.1016/j.ypmed.2011.11.012

Wang, G. D., Fan, R. X., Zhai, W., Liu, F., Wang, L., Zhong, L., Wu, H., Yang, H. C., Wu, S. F., Zhu, C. L., Li, Y., Gao, Y., Ge, R. L., Wu, C. I., & Zhang, Y. P. (2014). Genetic convergence in the adaptation of dogs and humans to the high-altitude environment of the Tibetan Plateau. *Genome Biology and Evolution*, *6*(8), 2122–2128. https://doi.org/10.1093/gbe/evu162

Watowich, M. M., MacLean, E. L., Hare, B., Call, J., Kaminski, J., Miklósi, Á., & Snyder-Mackler, N. (2020). Age influences domestic dog cognitive performance independent of average breed lifespan. *Animal Cognition*, *0123456789*. https://doi.org/10.1007/s10071-020-01385-0

Wilkins, A. S., Wrangham, R. W., & Tecumseh Fitch, W. (2014). The "domestication syndrome" in mammals: A unified explanation based on neural crest cell behavior and genetics. *Genetics*, *197*(3), 795–808. https://doi.org/10.1534/genetics.114.165423

Xu, J., Becker, A. A. M. J., Luo, Y., Zhang, W., Ge, B., Leng, C., Wang, G., Ding, L., Wang, J., Fu, X., & Janssens, G. P. J. (2021). The fecal microbiota of dogs switching to a raw diet only partially converges to that of wolves. *Frontiers in Microbiology*, *12*(September). https://doi.org/10.3389/fmicb.2021.701439

Yarlagadda, K., Zachwieja, A. J., De Flamingh, A., Phungviwatnikul, T., Rivera-Colon, A. G., Roseman, C., Shackelford, L., Swanson, K. S., & Malhi, R. S. (2022). Geographically diverse canid sampling provides novel insights into pre-industrial microbiomes. *Proceedings of the Royal Society B: Biological Sciences*, *289*(1974). https://doi.org/10.1098/rspb.2022.0052

Zeder, M. A. (2012). The domestication of animals. *Journal of Anthropological Research*, *68*(2), 161–190.

Zhang, Y., Hedo, R., Rivera, A., Rull, R., Richardson, S., & Tu, X. M. (2019). Post hoc power analysis: is it an informative and meaningful analysis? *General Psychiatry*, *32*(4), 3–6. https://doi.org/10.1136/gpsych-2019-100069

Appendix A

List of Questions Included in the Dognition Owner Survey

Appendix **A**: List of questions included in the Dognition owner survey.

Question	Timing	Verbiage	Answer Choices	Question Topics
q_20	Pre	When you laugh, does {dog_name} wag {hisher} tail?	Never, Seldom, Sometimes, Usually, Always	Communication, Empathy
q_21	Pre	When you cry, either in pain or sadness, does {dog_name} offer comfort (put {hisher} head on your lap, nudge with nose, etc.)?	Never, Seldom, Sometimes, Usually, Always	Communication, Empathy
q_22	Pre	Does {dog_name} ever "intervene" in an argument between other members of the household (put {hisher} head on your lap, nudge with nose, bark, etc.)?	Never, Seldom, Sometimes, Usually, Always	Communication, Empathy
q_23	Pre	Does {dog_name} ever seek eye contact with you and hold your gaze for more than a few seconds?	Never, Seldom, Sometimes, Usually, Always	Communication, Gaze sensitivity, Eye contact
q_24	Pre	If you point towards a toy or a ball, will {dog_name} follow your point to find it?	Never, Seldom, Sometimes, Usually, Always	Communication
q_25	Pre	If {dog_name} loses a toy or a ball, will {heshe} keep looking back to you for information while searching?	Never, Seldom, Sometimes, Usually, Always	Communication, Gaze sensitivity, Eye contact
q_26	Pre	Does {dog_name} learn new words and gestures with ease?	Never, Seldom, Sometimes, Usually, Always	Communication, Memory
q_27	Pre	If {dog_name} cannot reach something (a toy that rolled under the sofa, for example) does {heshe} try to get your attention for help?	Never, Seldom, Sometimes, Usually, Always	Communication, Gaze sensitivity
q_28	Pre	Does {dog_name} look up when you talk (either talking directly to {dog_name} or to someone else)?	Never, Seldom, Sometimes, Usually, Always	Human interest, Eye contact
q_29	Pre	Does {dog_name} come when {heshe}'s called no matter how far away/how engaged in an activity {heshe} is?	Never, Seldom, Sometimes, Usually, Always	Human interest, Training
q_30	Pre	Does {dog_name} understand you when you say "sit"?	Never, Seldom, Sometimes, Usually, Always	Communication
q_31	Pre	Does {dog_name} obey you when you say "sit"?	Never, Seldom, Sometimes, Usually, Always	Training
q_32	Pre	Does {dog_name} steal food from right under your nose?	Never, Seldom, Sometimes, Usually, Always	Gaze sensitivity, Training
q_33	Pre	Does {dog_name} steal food when you are distracted or not paying attention?	Never, Seldom, Sometimes, Usually, Always	Gaze sensitivity, Training
q_34	Pre	How often does {dog_name} chase or snap at flies or other insects?	Never, Seldom, Sometimes, Usually, Always	
q_35	Pre	How often does {dog_name} sniff other dogs' urine?	Never, Seldom, Sometimes, Usually, Always	Smell

q_36	Pre	Does {dog_name} spend most of {hisher} walks with {hisher} nose to the ground?	Never, Seldom, Sometimes, Usually, Always	Smell
q_37	Pre	If you put food in {dog_name}'s bowl while {heshe} is in another room, does {dog_name} come running immediately?	Never, Seldom, Sometimes, Usually, Always	Food motivation
q_38	Pre	How often does {dog_name} seem to hear things that you don't?	Never, Seldom, Sometimes, Usually, Always	Hearing
q_39	Pre	If you hide {dog_name}'s favorite toy where {heshe} can't get it, does {heshe} frequently return to where the toy is hidden for hours or even days afterwards?	Never, Seldom, Sometimes, Usually, Always	Memory
q_40	Pre	Does {dog_name} remember new commands or new words after you have only told {himher} once or twice?	Never, Seldom, Sometimes, Usually, Always	Communication, Memory
q_41	Pre	Does {dog_name} remember distant (human) relatives or acquaintances that only visit once or twice a year?	Never, Seldom, Sometimes, Usually, Always	Memory
q_42	Pre	How many words does {dog_name} know?	0-5, 6-10, 11-20, 21-50, More than 50	Communication, Memory
q_43	Pre	If {dog_name} has been scared or hurt by something in the past, does {heshe} now act nervously around similar objects?	Never, Seldom, Sometimes, Usually, Always	Memory
q_44	Pre	If {dog_name} knows you have food or a toy, but you show {himher} that one hand is empty, does {heshe} search the other hand?	Never, Seldom, Sometimes, Usually, Always	Reasoning
q_45	Pre	Does {dog_name} ever escape from your yard through a door or a gate, even though it is shut?	Never, Seldom, Sometimes, Usually, Always	Reasoning
q_46	Pre	Does {dog_name} ever learn to solve a problem by watching you?	Never, Seldom, Sometimes, Usually, Always	Communication, Reasoning
q_47	Pre	Does {dog_name} know when someone in your household arrives home before they walk in the door? For instance, can {heshe} recognize the sound of your car or the school bus or the jingle of keys in the door?	Never, Seldom, Sometimes, Usually, Always	Memory, Reasoning
q_48	Pre	Does {dog_name} get {hisher} leash tangled around trees or posts while you are walking?	Never, Seldom, Sometimes, Usually, Always	Reasoning
q_77	Pre	Does {dog_name} tolerate you taking or touching {hisher} food?	Never, Seldom, Sometimes, Usually, Always	
q_49	Post	While you are away from home for any period of time, does {dog_name} vocalize excessively (barking, howling, or whining)?	Never, Seldom, Sometimes, Usually, Always	Human interest, Training
q_50	Post	While you are away from home for any period of time, does {dog_name} express any destructive behavior (scratching, chewing, etc.)?	Never, Seldom, Sometimes, Usually, Always	Gaze sensitivity, Training
q_51	Post	Do your neighbors complain of whining, barking or howling while you are away and {dog_name} is alone?	Never, Seldom, Sometimes, Usually, Always	Human interest, Training
q_52	Post	Does {dog_name} get up and follow you when you leave the room?	Never, Seldom, Sometimes, Usually, Always	Human interest

q_53	Post	Does {dog_name} choose to be in proximity to you, even when having free range of the house?	Never, Seldom, Sometimes, Usually, Always	Human interest
q_54	Post	How much excitement does {dog_name} display when you give {himher} a new toy?	None, Mild, Moderate, Considerable, Extreme	
q_55	Post	When travelling in the car, how much excitement does {dog_name} display when arriving at your destination?	None, Mild, Moderate, Considerable, Extreme	
q_56	Post	How much excitement does {dog_name} display when you pull out {hisher} leash?	None, Mild, Moderate, Considerable, Extreme	
q_57	Post	How much excitement/reaction does {dog_name} show when a visitor knocks on the door?	None, Mild, Moderate, Considerable, Extreme	
q_58	Post	How much interest/excitement does {dog_name} display when {heshe} sees other dogs?	None, Mild, Moderate, Considerable, Extreme	
q_59	Post	How much interest/excitement does {dog_name} display when {heshe} sees a small, furry creature?	None, Mild, Moderate, Considerable, Extreme	
q_60	Post	How much excitement does {dog_name} display when you start to play with {himher}?	None, Mild, Moderate, Considerable, Extreme	
q_62	Post	Does {dog_name} ever show signs of aggression towards new people?	Never, Seldom, Sometimes, Usually, Always	
q_63	Post	Does {dog_name} ever show signs of aggression towards new dogs?	Never, Seldom, Sometimes, Usually, Always	
q_64	Post	Does {dog_name} ever show signs of aggression towards new children?	Never, Seldom, Sometimes, Usually, Always	
q_65	Post	Does {dog_name} ever show signs of aggression towards familiar people?	Never, Seldom, Sometimes, Usually, Always	
q_66	Post	Does {dog_name} ever show signs of aggression towards familiar dogs?	Never, Seldom, Sometimes, Usually, Always	
q_67	Post	Does {dog_name} ever show signs of aggression towards familiar children?	Never, Seldom, Sometimes, Usually, Always	
q_68	Post	Does {dog_name} ever show signs of aggression towards dogs bigger than {himher}?	Never, Seldom, Sometimes, Usually, Always	
q_69	Post	How much fear or anxiety does {dog_name} display in response to fireworks?	None, Mild, Moderate, Considerable, Extreme	
q_70	Post	How much fear or anxiety does {dog_name} display in response to thunder?	None, Mild, Moderate,	

			Considerable, Extreme	
q_71	Post	How much fear or anxiety does {dog_name} display in response to a smoke alarm?	None, Mild, Moderate, Considerable, Extreme	
q_72	Post	How much fear or anxiety does {dog_name} display in response to a slamming door?	None, Mild, Moderate, Considerable, Extreme	
q_73	Post	How much caution does {dog_name} display in response to new toys?	None, Mild, Moderate, Considerable, Extreme	
q_74	Post	How much caution does {dog_name} display in response to new furniture/appliances?	None, Mild, Moderate, Considerable, Extreme	
q_75	Post	How much caution does {dog_name} display in response to new food?	None, Mild, Moderate, Considerable, Extreme	
q_76	Post	How much caution does {dog_name} display in response to new places?	None, Mild, Moderate, Considerable, Extreme	
q_78	Post	Does {dog_name} react with jealousy when you come into physical contact with someone else?	Never, Seldom, Sometimes, Usually, Always	Human interest
q_79	Post	Would {dog_name} sleep in your bed with you if not told otherwise?	Never, Seldom, Sometimes, Usually, Always	Human interest
q_80	Post	How often does {dog_name} run away/escape from home?	Never, Seldom, Sometimes, Usually, Always	Human interest
q_81	Post	If you were to hand {dog_name} off to a stranger momentarily, how much anxiety or discomfort would {heshe} display?	None, Mild, Moderate, Considerable, Extreme	Human interest
q_82	Post	Does {dog_name} tend to ignore you if you don’t have food or a toy?	Never, Seldom, Sometimes, Usually, Always	Human interest
q_83	Post	Does {dog_name} ever show signs of aggression towards dogs smaller than {himher}?	Never, Seldom, Sometimes, Usually, Always	
q_84	Post	Does {dog_name} welcome anyone into your house, even if they are a stranger?	Never, Seldom, Sometimes, Usually, Always	Human interest
q_85	Post	Does {dog_name} like to play chase games with other dogs?	Never, Seldom, Sometimes, Usually, Always	
q_86	Post	In general, is {dog_name} good with children?	Never, Seldom, Sometimes, Usually, Always	
q_87	Post	Does {dog_name} ever hide when you have groups of people over at your house?	Never, Seldom, Sometimes, Usually, Always	

q_88	Post	Does {dog_name} show interest in other dogs?	Never, Seldom, Sometimes, Usually, Always	
q_89	Post	Does {dog_name} show interest in other people?	Never, Seldom, Sometimes, Usually, Always	Human interest
q_90	Post	Does {dog_name} act interested in/positively to new adults?	Never, Seldom, Sometimes, Usually, Always	
q_91	Post	Does {dog_name} act interested in/positively to new children?	Never, Seldom, Sometimes, Usually, Always	
q_92	Post	Does {dog_name} act interested in new pets (non-dog)?	Never, Seldom, Sometimes, Usually, Always	
q_93	Post	Does {dog_name} ever get easily startled?	Never, Seldom, Sometimes, Usually, Always	
q_94	Post	Does {dog_name} ever investigate an unexpected occurrence?	Never, Seldom, Sometimes, Usually, Always	
q_95	Post	Does {dog_name} ever play with strangers?	Never, Seldom, Sometimes, Usually, Always	
q_96	Post	In general, are people safely allowed to touch {dog_name}?	Never, Seldom, Sometimes, Usually, Always	
q_97	Post	Is {dog_name} wary of new people entering the household?	Never, Seldom, Sometimes, Usually, Always	
q_98	Post	Is {dog_name} wary of new dogs entering the household?	Never, Seldom, Sometimes, Usually, Always	
q_99	Post	Does {dog_name} get easily startled by unfamiliar objects during {hisher} walk?	Never, Seldom, Sometimes, Usually, Always	
q_117	Post	How many other dogs are in the household?	None, 1, 2, 3, 4, More	
q_118	Post	How old was {dog_name} when {heshe} became part of the family?	Newborn, 1-3 Months, 4-6 Months, 7-12 Months, 1-2 years, 2 years or more	
q_124	Post	Does {dog_name} have a tuxedo pattern? (a white patch on {hisher} chest)	Yes, No	
q_125	Post	Do {dog_name}'s ears naturally stand up?	Yes, No	
q_129	Post	How much training has {dog_name} recieved?	None, Little, Some, Substantial	Training
q_130	Post	Has {dog_name} attended a puppy class?	Yes, No	Training
q_131	Post	Has {dog_name} attended an obedience class?	Yes, No	Training
q_132	Post	Has {dog_name} ever competed in a K9 nose work competition?	Yes, No	Training, Smell
q_133	Post	Is {dog_name} an active service dog?	Yes, No	Training
q_134	Post	Is {dog_name} an active therapy dog?	Yes, No	Training
q_135	Post	Does {dog_name} have any hearing impairments?	Yes, No	Hearing

q_136	Post	Does {dog_name} have any sight impairments?	Yes, No	Vision
q_137	Post	Does {dog_name} have any mobility impairments?	Yes, No	
q_139	Post	Is {dog_name} up to date on {hisher} vaccines?	Yes, No	
q_140	Post	Is {dog_name} on any medications (besides a daily dose of treats)?	Yes, No	
q_141	Post	Is {dog_name} on flea medication?	Yes, No	
q_142	Post	Is {dog_name} on heartworm medication?	Yes, No	
q_143	Post	How many times a day is {dog_name} fed?	Once a day, 2 times a day, 3 times a day, {heshe} always has food available	
q_144	Post	How frequently does {dog_name} go to doggy day care?	Never, Only for vacations, Every Week	
q_145	Post	How often does {dog_name} go on walks?	Multiple times a day, Once a day, A couple times a week, A couple times a month, Rarely, Never	
q_146	Post	How often does {dog_name} have access to a back yard?	Always, Multiple times a day, Once a day, A couple times a week, A couple times a month, Rarely	
q_148	Post	How many people live with {dog_name} aside from yourself?	None, 1, 2, 3, 4, More	
q_149	Post	How many children live in the household currently?	None, 1, 2, 3, 4, More	
q_150	Post	Has {dog_name} competed in an agility competition?	Yes, No	
q_151	Post	Has {dog_name} competed in any dog shows?	Yes, No	
q_152	Post	Does {dog_name} live with other non-dog pets?	Yes, No	
q_154	Post	How many toys does {dog_name} currently have?	0, 1-10, 11-20, 20+	
q_155	Post	Does {dog_name} have any behavioral issues that stop either you or {dog_name} from socializing?	Yes, No	
q_157	Post	Has {dog_name} been trained as a hunting dog?	Yes, No	Training, Smell
q_158	Post	Does {dog_name} live with any of {hisher} blood related brothers or sisters?	Yes, No	
q_159	Post	How food motivated would you say {dog_name} is?	Extremely, Very, Somewhat, Partially, Not at All	Food motivation
q_160	Post	How many dogs have you owned before {dog_name}?	0, 1, 2, 3, 4, 5, 6+	
q_161	Post	Do you purchase {dog_name} presents for {hisher} birthday?	Yes, No	
q_162	Post	Does {dog_name} have a favorite toy?	Yes, No	
q_163	Post	How often do you have to discipline {dog_name}?	Every day, A couple times a week, A couple times a month, Rarely, Never	Self-control

q_164	Post	Was {dog_name} trained with a clicker?	Yes, No	Training
q_168	Post	Has {dog_name} ever been bitten by another dog?	Yes, No	
q_177	Post	How much of a picky eater is {dog_name}?	Extremely picky, Very picky, Moderately picky, Not very picky, Eats anything	Food motivation
q_178	Post	Do you have to do anything special to encourage {dog_name} to eat?	Yes, No, Sometimes	Food motivation
q_179	Post	Is {dog_name} crate trained?	Yes, No	
q_180	Post	Where does {dog_name} stay when you are not home?	{Heshe} has free reign of the neighborhood, {Heshe} has to stay in the yard, {Heshe} has to stay indoors, {Heshe} has to stay in a specific room, {Heshe} has to stay in {hisher} crate, Other	
q_181	Post	Does {dog_name} have a microchip?	Yes, No	
q_187	Post	How fast does {dog_name} eat {hisher} meals?	Done within 1 minute, Done within 5 minutes, Done within 10 minutes, Done within 25 minutes, Takes longer than 25 minutes, Grazes from food bowl, Other	Food motivation
q_189	Post	Does {dog_name} like toys with squeakers more than other toys?	Yes, No	
q_190	Post	Does {dog_name} have a dog outside your household who {heshe} prefers to interact with over other dogs?	Yes, No	
q_191	Post	Is {dog_name} a vegetarian?	Yes, No	
q_193	Post	Does {dog_name} prefer to eat {hisher} meal when you or other family members are present?	No preference, Sometimes, Usually, Always	Human interest
q_194	Post	Do you have a meal ritual with {dog_name} (something you do almost every time {heshe} eats)?	Yes, No	
q_205	Post	Does {dog_name} seek you, or other family members, out to be present when {heshe} eats {hisher} meal?	Never, Seldom, Sometimes, Usually, Always	Human interest
q_206	Post	In the last few years have you noticed {dog_name} doing any of the following more often: pacing, staring at the wall, or getting stuck behind furniture?	Yes, No	

Appendix B

Statistical Tests from Dognition Eye Contact Task

Appendix **B**: Results of statistical tests from the Chapter 3 analysis of the Dognition eye contact task. For key to questions, see Appendix A. Results of the exploratory analysis are given on the left and for the conservative analysis on the right. Asterisks represent significance after applying a Bonferroni correction (dividing the significance threshold by 129 for the exploratory analysis and by 30 for the conservative analysis).

Question	**Predictions**	**Exploratory Analysis**				**Conservative Analysis**			
		n	**β**	**p**		**n**	**β**	**p**	
q_20	Empathy	14554	1.155	3.01E-08	***	4138	1.326	0.0007	*
q_21	Empathy	14435	1.214	6.3E-09	***	4138	1.728	2.79E-05	***
q_22	Empathy	12707	1.128	5.28E-07	***	4138	0.903	0.026348	
q_23	Eye contact	16265	2.735	8.29E-41	***	4138	2.784	6.46E-11	***
q_24		15927	3.069	3.3E-50	***	4138	3.31	1.42E-14	***
q_25	Eye contact	15160	2.189	4.03E-26	***	4138	2.475	1.77E-09	***
q_26		15640	1.681	1.04E-15	***	4138	2.395	4.06E-09	***
q_27		15929	2.136	1.41E-26	***	4138	1.959	3.74E-06	***
q_28	Eye contact	16284	2.172	2.04E-26	***	4138	2.911	2.78E-12	***
q_29	Human interest	16334	1.718	5.11E-17	***	4138	1.449	0.000376	*
q_30		16241	2.999	7.17E-37	***	4138	3.723	1.8E-13	***
q_31		16292	2.502	6.04E-29	***	4138	2.27	3.7E-07	***
q_32		16231	-0.693	0.000641		4138	-0.304	0.438739	
q_33		16066	-0.448	0.026249		4138	-0.136	0.732301	
q_34		16051	-1.546	1.91E-14	***	4138	-1.688	2.81E-05	***
q_35		15874	1.068	3.19E-07	***	4138	0.939	0.023533	
q_36		16268	-0.175	0.384832		4138	-0.018	0.963587	
q_37	Food motivation	15691	2.661	1.64E-39	***	4138	2.586	1.07E-10	***
q_38		16062	-0.043	0.830354		4138	0.096	0.81246	
q_39		11055	1.625	1.46E-11	***	4138	1.713	2.51E-05	***
q_40		15118	0.858	3.85E-05	**	4138	1.515	0.000193	**
q_41		13240	2.545	7.93E-28	***	4138	2.757	6.42E-12	***
q_42		15619	3.933	3.23E-77	***	4138	3.37	2.03E-15	***
q_43		13919	0.449	0.039927		4138	0.315	0.438224	
q_44		14105	2.369	2.09E-27	***	4138	2.916	7E-13	***
q_45		13849	-1.159	1.49E-07	***	4138	-1.616	4.19E-05	**
q_46		12682	1.19	3.07E-07	***	4138	1.299	0.000953	*
q_47		15779	1.478	6.85E-13	***	4138	1.544	0.000396	*
q_48		15940	-1.823	2.28E-18	***	4138	-1.643	3.44E-05	**
q_77		16243	0.55	0.012339		4138	0.731	0.080381	
q_49	Human interest	4849	-1.783	3.14E-06	***				

q_50		5088	-2.989	9.4E-16	***				
q_51	Human interest	5259	-0.869	0.021509					
q_52	Human interest	4146	0.128	0.749132					
q_53	Human interest	4149	1.39	0.000505					
q_54		4799	0.759	0.04409					
q_55		4068	0.04	0.918902					
q_56		4207	-0.068	0.859494					
q_57		4303	0.168	0.661846					
q_58		4290	-2.273	4.72E-09	***				
q_59		4212	-1.601	4.04E-05	**				
q_60		5108	-0.306	0.396392					
q_62		5073	-1.164	0.001029					
q_63		5055	-0.251	0.48315					
q_64		4746	-0.959	0.008218					
q_65		4136	-1.525	4.09E-05	**				
q_66		4054	-1.302	0.000653					
q_67		3598	-1.568	7.81E-05	*				
q_68		3984	-0.807	0.044792					
q_69		4058	-1.023	0.011598					
q_70		4569	-1.123	0.003997					
q_71		3293	-0.55	0.223299					
q_72		4604	-1.08	0.004584					
q_73		4127	-1.385	0.001528					
q_74		3792	-0.883	0.045187					
q_75		4097	-1.803	4.77E-05	**				
q_76		4184	-1.697	2.46E-05	**				
q_78	Human interest	4939	0.396	0.286818					
q_79	Human interest	3894	0.744	0.06758					
q_80	Human interest	4818	-1.586	5.35E-05	**				
q_81	Human interest	4050	-0.803	0.043858					
q_82	Human interest	4314	-0.839	0.030454					
q_83		4026	-0.965	0.014431					
q_84	Human interest	4092	0.672	0.08995					
q_85		6913	-1.986	8.28E-11	***				
q_86		3850	0.402	0.312729					
q_87		3794	-0.964	0.024879					
q_88		4966	-1.568	2.02E-05	**				
q_89	Human interest	4960	0.74	0.043018					
q_90		4794	1.334	0.000335	*				
q_91		4005	0.427	0.275635					
q_92		2486	0.187	0.724749					

q_93		4930	1.348	0.00018	*				
q_94		3788	0.761	0.070704					
q_95		3960	-0.164	0.685592					
q_96		4125	0.684	0.089976					
q_97		5481	1.22	0.000389					
q_98		4686	0.287	0.436425					
q_99		6092	1.523	3.32E-06	***				
q_117		7779	-0.84	0.007149					
q_118		4688	0.145	0.694164					
q_124		3775	-1.093	0.007785					
q_125		3801	-1.844	7.47E-06	***				
q_129		3507	2.47	8.9E-08	***				
q_130		3176	1.361	0.002392					
q_131		3344	2.177	8.51E-07	***				
q_132		3437	0.606	0.150719					
q_133		3433	0.651	0.16458					
q_134		3429	1.248	0.002128					
q_135		3140	1.16	0.045885					
q_136		3091	0.098	0.841699					
q_137		3189	0.302	0.52206					
q_139		3099	0.475	0.428761					
q_140		3132	1.296	0.003487					
q_141		3100	-0.272	0.556956					
q_142		3086	0.831	0.078127					
q_143		3089	-0.054	0.912148					
q_144		3082	-0.954	0.026653					
q_145		3050	0.227	0.635108					
q_146		2861	0.341	0.453193					
q_148		2997	-1.389	0.004426					
q_149		2979	-0.536	0.292987					
q_150		3355	1.731	2.5E-05	**				
q_151		3299	1.617	0.00011	*				
q_152		2920	-0.832	0.07404					
q_154		2377	0.934	0.065701					
q_155		2831	-0.393	0.395935					
q_157		3313	-0.11	0.799012					
q_158		2812	0.353	0.493453					
q_159	Food motivation	2809	2.715	4.01E-08	***				
q_160		2784	-0.431	0.366692					
q_161		2242	0.61	0.244574					
q_162		2301	0.192	0.711257					

q_163		2216	-1.611	0.002241					
q_164		3199	0.14	0.742926					
q_168		1869	1.027	0.072407					
q_177	Food motivation	4172	-2.084	1.05E-07	***				
q_178	Food motivation	3849	1.735	1.8E-05	**				
q_179		3246	0.312	0.487796					
q_180		2791	-1.501	0.00196					
q_181		3017	0.094	0.84237					
q_187	Food motivation	2770	2.164	6.38E-06	***				
q_189		2343	0.603	0.254683					
q_190		2315	-0.15	0.775792					
q_191		2608	0.564	0.267215					
q_193	Human interest	2312	-1.015	0.05139					
q_194		2420	-0.052	0.919355					
q_205	Human interest	4075	-0.957	0.01439					
q_206		3940	-0.005	0.989897					

Appendix C

Statistical Tests from Dognition Arm Pointing Task

Appendix **C**: Results of statistical tests from the Chapter 3 analysis of the Dognition arm pointing task. For key to questions, see Appendix A. Results of the exploratory analysis are given on the left and for the conservative analysis on the right. Asterisks represent significance after applying a Bonferroni correction (dividing the significance threshold by 129 for the exploratory analysis and by 30 for the conservative analysis).

Question	**Predictions**	**Exploratory Analysis**				**Conservative Analysis**			
		n	**β**	**p**		**n**	**β**	**p**	
q_20	Communication (emotional)	10156	0.051	7.57E-10	***	2877	0.058	0.00019	**
q_21	Communication (emotional)	10030	0.021	0.010634		2877	0.023	0.149189	
q_22	Communication (emotional)	8783	0.046	2.48E-07	***	2877	0.062	0.000111	**
q_23	Communication (emotional)	11317	0.037	6.52E-06	***	2877	0.045	0.008423	
q_24	Communication (gestural)	11094	0.103	1.55E-35	***	2877	0.112	4.94E-11	***
q_25	Communication	10592	0.04	1.03E-06	***	2877	0.041	0.012277	
q_26	Communication (gestural)	10944	0.085	6.97E-24	***	2877	0.117	6.72E-13	***
q_27	Communication	11086	0.033	4.38E-05	**	2877	0.034	0.038974	
q_28	Human interest	11338	0.05	1.61E-09	***	2877	0.076	4.15E-06	***
q_29	Human interest	11376	0.085	1.22E-24	***	2877	0.124	3.18E-14	***
q_30	Communication (verbal)	11333	0.079	3.24E-15	***	2877	0.109	2.57E-07	***
q_31		11362	0.095	6.22E-25	***	2877	0.143	5.87E-15	***
q_32		11311	-0.036	9.94E-06	**	2877	-0.046	0.003477	
q_33		11191	-0.044	4.64E-08	***	2877	-0.059	0.000146	**
q_34		11179	-0.016	0.043609		2877	-0.028	0.083539	
q_35		11077	-0.01	0.24854		2877	-0.006	0.715628	
q_36		11347	-0.013	0.105575		2877	-0.042	0.009341	
q_37		10929	0.032	5.67E-05	**	2877	0.04	0.01344	
q_38		11172	0.016	0.051025		2877	-0.002	0.897736	
q_39		7738	0.031	0.001063		2877	0.036	0.025697	
q_40	Communication (verbal)	10571	0.074	4.68E-19	***	2877	0.105	1.3E-10	***
q_41		9285	0.03	0.001585		2877	0.047	0.004281	
q_42	Communication (verbal)	10922	0.111	3.24E-37	***	2877	0.127	9.03E-13	***
q_43		9725	-0.008	0.342863		2877	-0.016	0.335485	
q_44		9847	0.038	1.32E-05	**	2877	0.04	0.012303	
q_45		9653	-0.036	5.05E-05	**	2877	-0.031	0.045829	
q_46	Communication	8870	0.06	1.36E-10	***	2877	0.053	0.00084	*

q_47		10972	0.014	0.097302		2877	-0.004	0.80079	
q_48		11124	-0.055	8.56E-11	***	2877	-0.067	2.12E-05	***
q_77		11321	0.019	0.027035		2877	0.022	0.188846	
q_49	Human interest	3681	-0.041	0.006192					
q_50		3846	-0.031	0.030811					
q_51	Human interest	3991	-0.023	0.132263					
q_52	Human interest	3127	0.025	0.111932					
q_53	Human interest	3128	0.008	0.59443					
q_54		3619	0.01	0.495821					
q_55		3077	0.001	0.949769					
q_56		3178	-0.019	0.208492					
q_57		3254	-0.009	0.566301					
q_58		3247	-0.035	0.020527					
q_59		3189	-0.024	0.120037					
q_60		3860	-0.01	0.462461					
q_62		3835	0.004	0.745502					
q_63		3832	-0.036	0.00957					
q_64		3598	-0.009	0.503472					
q_65		3122	-0.001	0.924085					
q_66		3069	-0.007	0.636113					
q_67		2719	-0.003	0.860257					
q_68		3009	-0.016	0.299262					
q_69		3057	0.004	0.78977					
q_70		3458	-0.007	0.66338					
q_71		2500	-0.015	0.387858					
q_72		3485	-0.02	0.188987					
q_73		3124	0.012	0.48058					
q_74		2874	-0.008	0.643202					
q_75		3098	-0.024	0.162903					
q_76		3167	-0.025	0.113218					
q_78	Human interest	3724	-0.026	0.072041					
q_79	Human interest	2926	-0.014	0.386968					
q_80	Human interest	3642	-0.062	4.13E-05	**				
q_81	Human interest	3066	-0.002	0.879999					
q_82	Human interest	3261	-0.039	0.010864					
q_83		3047	-0.038	0.014442					
q_84	Human interest	3082	0.018	0.243943					
q_85		5285	-0.004	0.723221					
q_86		2912	0.028	0.074729					
q_87		2867	-0.036	0.034108					
q_88		3758	0.002	0.908805					

q_89	Human interest	3750	-0.021	0.141016					
q_90		3617	0.006	0.701742					
q_91		3035	0.004	0.809917					
q_92		1855	0.015	0.470098					
q_93		3725	0.031	0.026372					
q_94		2863	0.023	0.168621					
q_95		2975	-0.019	0.22239					
q_96		3112	0.01	0.532383					
q_97		4165	0.013	0.33724					
q_98		3552	0.043	0.002471					
q_99		4628	0.039	0.002044					
q_117		5841	0.028	0.024595					
q_118		3670	-0.042	0.003432					
q_124		2980	0.002	0.892391					
q_125		2988	-0.026	0.100115					
q_129		2762	0.119	7.48E-11	***				
q_130		2510	0.029	0.095519					
q_131		2639	0.037	0.031716					
q_132		2713	0.019	0.23103					
q_133		2705	0.084	1.67E-05	**				
q_134		2702	0.025	0.11355					
q_135		2475	0.019	0.410113					
q_136		2439	0.009	0.64079					
q_137		2510	-0.001	0.940342					
q_139		2443	0.005	0.845138					
q_140		2467	-0.012	0.475332					
q_141		2441	-0.036	0.049922					
q_142		2432	-0.02	0.276178					
q_143		2432	-0.001	0.94405					
q_144		2426	-0.039	0.018562					
q_145		2401	0.016	0.411551					
q_146		2258	0.023	0.188026					
q_148		2365	-0.002	0.916566					
q_149		2349	-0.008	0.670659					
q_150		2648	0.079	1.13E-06	***				
q_151		2607	0.064	0.000104	*				
q_152		2300	0.031	0.087311					
q_154		1902	0.041	0.039028					
q_155		2240	-0.05	0.004825					
q_157		2621	0.026	0.127535					
q_158		2224	0.048	0.025114					

q_159		2220	0.049	0.012359					
q_160		2198	0.051	0.006073					
q_161		1805	-0.032	0.12327					
q_162		1843	-0.019	0.337792					
q_163		1772	-0.036	0.076094					
q_164		2534	0.047	0.00386					
q_168		1508	0.008	0.729287					
q_177		3334	-0.023	0.118666					
q_178		3064	0.045	0.003968					
q_179		2592	0.022	0.198844					
q_180		2229	-0.033	0.068962					
q_181		2410	0.014	0.424316					
q_187		2206	0.048	0.010421					
q_189		1879	0	0.982751					
q_190		1861	0.02	0.321468					
q_191		2085	-0.004	0.861038					
q_193	Human interest	1829	-0.001	0.972086					
q_194		1918	-0.021	0.296913					
q_205	Human interest	3251	0.001	0.925534					
q_206		3135	-0.021	0.196482					

Appendix D

Statistical Tests from Dognition Foot Pointing Task

Appendix **D**: Results of statistical tests from the Chapter 3 analysis of the Dognition foot pointing task. For key to questions, see Appendix A. Results of the exploratory analysis are given on the left and for the conservative analysis on the right. Asterisks represent significance after applying a Bonferroni correction (dividing the significance threshold by 129 for the exploratory analysis and by 30 for the conservative analysis).

Question	**Predictions**	**Exploratory Analysis**				**Conservative Analysis**			
		n	**β**	**p**		**n**	**β**	**p**	
q_20	Communication (emotional)	9527	0.031	0.000303	*	2690	0.064	8.15E-05	**
q_21	Communication (emotional)	9380	0.039	3.92E-06	***	2690	0.043	0.010583	
q_22	Communication (emotional)	8211	0.047	2.61E-07	***	2690	0.032	0.054375	
q_23	Communication (emotional)	10601	0.044	2.63E-07	***	2690	0.061	0.00046	*
q_24	Communication (gestural)	10392	0.102	8.02E-33	***	2690	0.099	3.14E-08	***
q_25	Communication	9921	0.057	1.28E-11	***	2690	0.056	0.000841	*
q_26	Communication (gestural)	10263	0.068	3.54E-15	***	2690	0.074	1.06E-05	***
q_27	Communication	10389	0.055	1.45E-11	***	2690	0.021	0.226423	
q_28	Human interest	10620	0.047	2.96E-08	***	2690	0.052	0.002457	
q_29	Human interest	10654	0.052	6.97E-10	***	2690	0.088	1.7E-07	***
q_30	Communication (verbal)	10612	0.074	8.31E-13	***	2690	0.118	1.16E-07	***
q_31		10641	0.062	1.24E-10	***	2690	0.095	6.08E-07	***
q_32		10592	-0.039	4.12E-06	***	2690	-0.043	0.008109	
q_33		10480	-0.043	1.72E-07	***	2690	-0.071	1.29E-05	***
q_34		10476	0.019	0.024613		2690	-0.001	0.96575	
q_35		10381	0.005	0.589324		2690	0.027	0.11138	
q_36		10629	0.008	0.359073		2690	0.004	0.802147	
q_37		10231	0.016	0.053637		2690	0.031	0.066605	
q_38		10461	0.024	0.004279		2690	0.02	0.224551	
q_39		7273	0.059	1.66E-09	***	2690	0.055	0.001058	*
q_40	Communication (verbal)	9916	0.052	9.99E-10	***	2690	0.063	0.000175	**
q_41		8678	0.033	0.000659		2690	0.028	0.097088	
q_42	Communication (verbal)	10223	0.107	1.97E-32	***	2690	0.108	2.7E-09	***
q_43		9119	0.014	0.104307		2690	-0.011	0.519353	
q_44		9228	0.051	1.01E-08	***	2690	0.069	3.04E-05	***
q_45		9034	-0.018	0.047054		2690	-0.025	0.132586	
q_46	Communication	8300	0.063	3.85E-11	***	2690	0.051	0.00188	

q_47		10271	0.049	7.45E-09	***	2690	0.036	0.044138	
q_48		10424	-0.036	3.22E-05	**	2690	-0.045	0.005918	
q_77		10606	0.005	0.598108		2690	-0.008	0.634558	
q_49	Human interest	3473	-0.029	0.063676					
q_50		3631	-0.035	0.015053					
q_51	Human interest	3773	-0.024	0.119063					
q_52	Human interest	2943	0.014	0.374989					
q_53	Human interest	2944	0.005	0.769484					
q_54		3413	0.049	0.001322					
q_55		2898	0.024	0.126258					
q_56		2997	0.029	0.063753					
q_57		3066	0.032	0.034022					
q_58		3060	-0.02	0.202847					
q_59		3005	0.035	0.0256					
q_60		3645	0.033	0.022937					
q_62		3620	0.008	0.589864					
q_63		3617	0.034	0.017707					
q_64		3389	0.01	0.494678					
q_65		2940	0.005	0.755868					
q_66		2890	0.007	0.646242					
q_67		2552	0.014	0.361043					
q_68		2837	0.037	0.02332					
q_69		2892	-0.013	0.438783					
q_70		3262	-0.009	0.556578					
q_71		2368	0.006	0.757553					
q_72		3290	-0.014	0.362642					
q_73		2942	0.012	0.48625					
q_74		2710	-0.012	0.489574					
q_75		2919	0.01	0.597855					
q_76		2984	-0.025	0.118379					
q_78	Human interest	3512	0.017	0.263053					
q_79	Human interest	2754	-0.011	0.511217					
q_80	Human interest	3435	-0.009	0.57191					
q_81	Human interest	2888	0.003	0.837021					
q_82	Human interest	3075	-0.023	0.137106					
q_83		2867	0.012	0.450567					
q_84	Human interest	2899	-0.011	0.47296					
q_85		5022	-0.017	0.152863					
q_86		2737	-0.008	0.635008					
q_87		2689	-0.022	0.216333					
q_88		3550	0.001	0.936127					

q_89	Human interest	3542	-0.007	0.609453					
q_90		3411	0.004	0.76309					
q_91		2859	-0.016	0.312208					
q_92		1749	0.026	0.220826					
q_93		3516	0.021	0.135538					
q_94		2699	0.067	5.61E-05	**				
q_95		2803	0.014	0.39192					
q_96		2929	0.018	0.243831					
q_97		3940	-0.007	0.617135					
q_98		3358	-0.033	0.022343					
q_99		4387	-0.005	0.698895					
q_117		5573	-0.018	0.140023					
q_118		3540	-0.019	0.187214					
q_124		2872	0.011	0.490478					
q_125		2881	0.015	0.362871					
q_129		2664	0.058	0.001797					
q_130		2418	0.007	0.693875					
q_131		2547	0.007	0.69138					
q_132		2618	0.025	0.125746					
q_133		2609	0.054	0.004672					
q_134		2606	0.045	0.00547					
q_135		2389	0.028	0.259321					
q_136		2350	0.015	0.459704					
q_137		2420	0.022	0.255015					
q_139		2358	-0.035	0.15397					
q_140		2381	0.008	0.635646					
q_141		2355	-0.01	0.587916					
q_142		2346	-0.014	0.449147					
q_143		2345	-0.015	0.435933					
q_144		2340	0	0.989163					
q_145		2317	-0.004	0.847989					
q_146		2175	0.002	0.911561					
q_148		2282	0.002	0.902027					
q_149		2268	0.011	0.576458					
q_150		2555	0.033	0.036045					
q_151		2514	0.017	0.289929					
q_152		2219	-0.005	0.763457					
q_154		1840	0.006	0.752084					
q_155		2161	0.002	0.909586					
q_157		2527	0.01	0.539527					
q_158		2144	-0.002	0.9418					

q_159		2141	0.022	0.265762					
q_160		2119	-0.032	0.086143					
q_161		1746	0	0.985359					
q_162		1782	0.026	0.206399					
q_163		1714	-0.021	0.301194					
q_164		2442	0.035	0.032008					
q_168		1458	0.046	0.040887					
q_177		3219	-0.017	0.267564					
q_178		2960	-0.011	0.482571					
q_179		2506	0.025	0.159071					
q_180		2159	-0.029	0.117612					
q_181		2333	-0.01	0.587174					
q_187		2136	0.011	0.562472					
q_189		1821	0.001	0.968122					
q_190		1804	-0.014	0.498931					
q_191		2015	-0.009	0.642706					
q_193	Human interest	1768	0.025	0.212251					
q_194		1853	0.017	0.399881					
q_205	Human interest	3099	0.036	0.021347					
q_206		2991	-0.041	0.012992					

Appendix E

Statistical Tests from Dognition Gaze Sensitivity to Back Turned Task

Appendix **E**: Results of statistical tests from the Chapter 3 analysis of the Dognition gaze sensitivity to back turned task. For key to questions, see Appendix A. Results of the exploratory analysis are given on the left and for the conservative analysis on the right. Asterisks represent significance after applying a Bonferroni correction (dividing the significance threshold by 129 for the exploratory analysis and by 30 for the conservative analysis).

Question	**Predictions**	**Exploratory Analysis**				**Conservative Analysis**		
		n	**β**	**p**		**n**	**β**	**p**
q_20		6815	-0.297	0.263113		1901	-0.209	0.668132
q_21		6666	-0.374	0.162082		1901	-0.425	0.411902
q_22		5799	0.307	0.286623		1901	0.283	0.571835
q_23	Gaze sensitivity	7553	-0.063	0.813241		1901	0.465	0.380281
q_24		7401	-0.068	0.80139		1901	1.044	0.058208
q_25	Gaze sensitivity	7102	0.278	0.28754		1901	1.031	0.043713
q_26		7326	0	0.99977		1901	0.178	0.732218
q_27	Gaze sensitivity	7405	0.433	0.089311		1901	0.718	0.170179
q_28		7567	0.189	0.474099		1901	0.956	0.06652
q_29		7593	-1.064	6.44E-05	**	1901	-0.982	0.056106
q_30		7566	-0.27	0.413809		1901	0.061	0.931884
q_31		7581	-0.634	0.036523		1901	-0.138	0.816121
q_32	Gaze sensitivity	7545	1.09	3.35E-05	**	1901	1.211	0.01292
q_33	Gaze sensitivity	7464	1.011	9.44E-05	*	1901	1.005	0.038568
q_34		7461	0.245	0.340557		1901	0.661	0.182411
q_35		7390	-0.489	0.068603		1901	-0.559	0.288525
q_36		7577	-0.066	0.797478		1901	0.303	0.544112
q_37		7281	0.127	0.624972		1901	0.485	0.333245
q_38		7452	0.121	0.638845		1901	0.432	0.388487
q_39		5203	0.468	0.114821		1901	0.95	0.058194
q_40		7076	0.128	0.6312		1901	0.746	0.144319
q_41		6178	-0.171	0.577952		1901	-0.649	0.212433
q_42		7274	-0.114	0.683033		1901	-0.263	0.636544
q_43		6468	0.394	0.154432		1901	0.642	0.198034
q_44		6562	0.75	0.007664		1901	1.591	0.001945
q_45		6399	0.309	0.299778		1901	0.216	0.667829
q_46		5929	0.666	0.024838		1901	1.374	0.005226
q_47		7298	-0.039	0.88278		1901	0.569	0.290957
q_48		7426	-0.185	0.498106		1901	0.675	0.174876
q_77		7554	-1.008	0.000564		1901	-0.694	0.208866

q_49	Human interest	2734	0.298	0.508038				
q_50	Gaze sensitivity	2851	0.762	0.080179				
q_51	Human interest	2971	1.184	0.008746				
q_52	Human interest	2305	0.598	0.188893				
q_53	Human interest	2308	0.432	0.357843				
q_54		2680	0.501	0.255763				
q_55		2269	-0.427	0.33907				
q_56		2359	-0.454	0.305794				
q_57		2408	0.556	0.204725				
q_58		2407	0.447	0.325129				
q_59		2367	0.24	0.592551				
q_60		2871	-0.178	0.673187				
q_62		2848	0.184	0.63889				
q_63		2849	0.118	0.770317				
q_64		2650	0.396	0.321372				
q_65		2308	0.459	0.250985				
q_66		2268	0.353	0.398286				
q_67		2001	0.517	0.229135				
q_68		2227	0.145	0.752921				
q_69		2281	0.629	0.184814				
q_70		2568	0.083	0.854174				
q_71		1864	0.098	0.847326				
q_72		2587	0.821	0.066022				
q_73		2310	-0.289	0.585486				
q_74		2129	1.517	0.002798				
q_75		2285	1.46	0.006661				
q_76		2341	1.322	0.004268				
q_78	Human interest	2758	0.759	0.081438				
q_79	Human interest	2151	1.056	0.025395				
q_80	Human interest	2702	0.036	0.939184				
q_81	Human interest	2267	0.175	0.702165				
q_82	Human interest	2417	1.57	0.000494				
q_83		2244	0.138	0.756181				
q_84		2273	-0.65	0.160322				
q_85		3948	0.177	0.611818				
q_86		2139	-1.1	0.017602				
q_87		2100	1.432	0.006839				
q_88		2794	-0.244	0.568366				
q_89		2786	-0.24	0.568461				
q_90		2681	-0.742	0.083087				
q_91		2248	-1.098	0.016289				

q_92		1341	0.58	0.341148				
q_93		2770	-1.331	0.001284				
q_94		2117	-0.307	0.524331				
q_95		2189	0.282	0.543381				
q_96		2296	-0.638	0.167483				
q_97		3101	-1.166	0.00307				
q_98		2638	-0.758	0.073416				
q_99		3458	-0.86	0.022949				
q_117		4300	-0.148	0.690617				
q_118		2860	-1.18	0.005269				
q_124		2335	0.122	0.787829				
q_125		2343	-0.344	0.459497				
q_129		2180	-0.437	0.428368				
q_130		1979	-0.093	0.855433				
q_131		2095	-0.46	0.362778				
q_132		2146	0.369	0.415204				
q_133		2141	0.07	0.89609				
q_134		2138	-0.959	0.029714				
q_135		1969	-0.576	0.377376				
q_136		1936	-0.043	0.940113				
q_137		1994	-0.385	0.470318				
q_139		1942	0.761	0.287287				
q_140		1959	-0.001	0.997689				
q_141		1940	0.396	0.451057				
q_142		1930	0.599	0.269733				
q_143		1931	-0.034	0.952915				
q_144		1926	0.87	0.065918				
q_145		1905	-0.168	0.765316				
q_146		1798	-1.504	0.00359				
q_148		1881	-0.235	0.676085				
q_149		1870	-0.299	0.622556				
q_150		2100	0.082	0.850201				
q_151		2065	0.111	0.81018				
q_152		1832	-0.897	0.08674				
q_154		1539	0.113	0.841835				
q_155		1783	0.416	0.421581				
q_157		2085	0.018	0.970087				
q_158		1770	1.194	0.044318				
q_159		1770	0.653	0.253256				
q_160		1751	-0.142	0.79228				
q_161		1466	-0.143	0.809301				

q_162		1492	-0.764	0.189568				
q_163		1432	1.556	0.008768				
q_164		2019	-0.215	0.648396				
q_168		1230	0.505	0.42586				
q_177		2646	0.219	0.614336				
q_178		2438	-0.754	0.092925				
q_179		2072	1.101	0.03112				
q_180		1785	1.186	0.022895				
q_181		1937	0.298	0.56983				
q_187		1773	-0.518	0.338241				
q_189		1515	0.395	0.490948				
q_190		1526	-0.381	0.499935				
q_191		1688	-0.588	0.297593				
q_193		1473	0.47	0.421227				
q_194		1545	-0.616	0.27876				
q_205		2396	0.163	0.725353				
q_206		2319	-0.099	0.843496				

Appendix F

Statistical Tests from Dognition Gaze Sensitivity to Eyes Closed Task

Appendix **F**: Results of statistical tests from the Chapter 3 analysis of the Dognition gaze sensitivity to eyes closed task. For key to questions, see Appendix A. Results of the exploratory analysis are given on the left and for the conservative analysis on the right. Asterisks represent significance after applying a Bonferroni correction (dividing the significance threshold by 129 for the exploratory analysis and by 30 for the conservative analysis).

Question	**Predictions**	**Exploratory Analysis**				**Conservative Analysis**		
		n	**β**	**p**		**n**	**β**	**p**
q_20		6815	-0.317	0.215179		1901	-0.251	0.601647
q_21		6665	-0.283	0.269521		1901	-0.746	0.143852
q_22		5798	0.448	0.106797		1901	0.289	0.557514
q_23	Gaze sensitivity	7552	-0.139	0.585797		1901	0.079	0.880208
q_24		7400	0.018	0.945932		1901	0.446	0.41192
q_25	Gaze sensitivity	7101	0.052	0.837255		1901	0.355	0.481342
q_26		7325	0.815	0.002075		1901	1.32	0.010112
q_27	Gaze sensitivity	7404	0.166	0.49996		1901	0.612	0.235652
q_28		7566	-0.153	0.548125		1901	0.128	0.803249
q_29		7592	-1.555	1.27E-09	***	1901	-1.435	0.004576
q_30		7565	0.506	0.111165		1901	0.581	0.410238
q_31		7580	-0.411	0.159433		1901	0.24	0.68222
q_32	Gaze sensitivity	7544	0.96	0.000148	*	1901	0.589	0.219974
q_33	Gaze sensitivity	7463	1.393	2.24E-08	***	1901	0.896	0.061277
q_34		7460	0.119	0.629677		1901	0.334	0.494181
q_35		7389	-0.393	0.128431		1901	-1.156	0.025871
q_36		7576	0.18	0.466968		1901	0.342	0.487109
q_37		7280	0.521	0.037532		1901	0.932	0.059207
q_38		7451	-0.282	0.256846		1901	0.07	0.887161
q_39		5202	-0.03	0.918231		1901	0.21	0.670469
q_40		7075	0.328	0.203842		1901	1.154	0.021763
q_41		6177	-0.236	0.425554		1901	-0.603	0.239457
q_42		7273	0.236	0.38042		1901	0.297	0.588078
q_43		6467	0.062	0.81515		1901	0.279	0.569721
q_44		6561	1.014	0.000198	*	1901	1.405	0.005464
q_45		6398	0.214	0.453973		1901	-0.006	0.991072
q_46		5928	0.549	0.053734		1901	1.123	0.020477
q_47		7297	-0.31	0.225895		1901	-0.248	0.640098
q_48		7425	0.041	0.876252		1901	1.035	0.034621
q_77		7553	-0.539	0.055731		1901	-0.41	0.451406
q_49	Human interest	2734	0.483	0.280514				

q_50	Gaze sensitivity	2851	0.735	0.088094				
q_51	Human interest	2971	-0.113	0.801931				
q_52	Human interest	2305	-0.071	0.875665				
q_53	Human interest	2308	0.232	0.618702				
q_54		2680	0.058	0.893193				
q_55		2269	-0.712	0.10799				
q_56		2359	-1.465	0.000895				
q_57		2408	-0.119	0.783667				
q_58		2407	0.47	0.294832				
q_59		2367	-0.528	0.232567				
q_60		2871	-0.093	0.824046				
q_62		2848	0.224	0.565879				
q_63		2849	-0.635	0.114398				
q_64		2650	0.205	0.606317				
q_65		2308	0.33	0.406403				
q_66		2268	0.158	0.703859				
q_67		2001	0.448	0.298735				
q_68		2227	-0.281	0.541627				
q_69		2281	0.057	0.901834				
q_70		2568	-0.038	0.932288				
q_71		1864	-0.722	0.152632				
q_72		2587	0.066	0.879339				
q_73		2310	-0.341	0.517369				
q_74		2129	0.625	0.216155				
q_75		2285	-0.051	0.923633				
q_76		2341	0.407	0.376574				
q_78	Human interest	2758	0.211	0.626523				
q_79	Human interest	2151	0.499	0.284536				
q_80	Human interest	2702	-0.056	0.903751				
q_81	Human interest	2267	-0.834	0.067183				
q_82	Human interest	2417	1.629	0.000261	*			
q_83		2244	0.093	0.832547				
q_84		2273	0.467	0.308369				
q_85		3948	0.779	0.022639				
q_86		2139	-0.166	0.719519				
q_87		2100	0.202	0.697273				
q_88		2794	0.595	0.159069				
q_89		2786	0.704	0.090357				
q_90		2681	0.789	0.060949				
q_91		2248	0.322	0.474175				
q_92		1341	-0.118	0.844839				

q_93		2770	-0.539	0.186759				
q_94		2117	0.161	0.738745				
q_95		2189	0.857	0.065499				
q_96		2296	-0.05	0.912717				
q_97		3101	-0.014	0.970408				
q_98		2638	0.19	0.64792				
q_99		3458	-0.33	0.372942				
q_117		4299	0.104	0.773514				
q_118		2860	-0.961	0.019431				
q_124		2335	0.209	0.639446				
q_125		2343	-0.38	0.400239				
q_129		2180	1.586	0.003157				
q_130		1979	0.955	0.055825				
q_131		2095	1.022	0.037269				
q_132		2146	0.187	0.671511				
q_133		2141	-0.256	0.622444				
q_134		2138	-0.581	0.174346				
q_135		1969	-0.724	0.2577				
q_136		1936	-0.887	0.107852				
q_137		1994	-0.526	0.314151				
q_139		1942	0.983	0.159366				
q_140		1959	-0.328	0.490342				
q_141		1940	0.251	0.627904				
q_142		1930	0.026	0.961593				
q_143		1931	-0.38	0.502553				
q_144		1926	0.322	0.489633				
q_145		1905	0.202	0.716885				
q_146		1798	-0.714	0.156472				
q_148		1881	-0.401	0.46585				
q_149		1870	-1.301	0.028802				
q_150		2100	-0.073	0.862718				
q_151		2065	-0.313	0.483237				
q_152		1832	-1.431	0.005146				
q_154		1539	-0.378	0.49422				
q_155		1783	0.362	0.478991				
q_157		2085	0.57	0.210771				
q_158		1770	0.286	0.620195				
q_159		1770	0.362	0.51382				
q_160		1751	-0.371	0.477321				
q_161		1466	-0.277	0.629622				
q_162		1492	-0.453	0.42557				

q_163		1432	2.202	0.000109	*			
q_164		2019	-0.257	0.570025				
q_168		1230	0.15	0.807274				
q_177		2646	-0.026	0.949789				
q_178		2438	-0.476	0.276979				
q_179		2072	0.557	0.259034				
q_180		1785	1.523	0.003195				
q_181		1937	0.123	0.810708				
q_187		1773	-0.719	0.167799				
q_189		1515	0.391	0.487863				
q_190		1526	0.071	0.896917				
q_191		1688	-0.909	0.099382				
q_193		1473	-0.745	0.18286				
q_194		1545	0.212	0.698701				
q_205		2395	-0.001	0.997503				
q_206		2318	0.475	0.319726				

Appendix G

Statistical Tests from Dognition Latency to Eat Prohibited Food When Unobserved

Appendix **G**: Results of statistical tests from the Chapter 3 analysis of the Dognition latency to eat prohibited food when unobserved. For key to questions, see Appendix A. Results of the exploratory analysis are given on the left and for the conservative analysis on the right. Asterisks represent significance after applying a Bonferroni correction (dividing the significance threshold by 129 for the exploratory analysis and by 30 for the conservative analysis).

Question	**Predictions**	**Exploratory Analysis**				**Conservative Analysis**			
		n	**β**	**p**		**n**	**β**	**p**	
q_20		6922	2.465	2.98E-09	***	1930	2.576	0.000806	*
q_21		6766	0.493	0.238766		1930	0.582	0.475415	
q_22		5887	0.316	0.481071		1930	0.396	0.615034	
q_23		7669	2.091	4.96E-07	***	1930	2.197	0.00851	
q_24		7512	4.75	1.62E-29	***	1930	4.094	2.3E-06	***
q_25	Eye contact	7207	1.223	0.002926		1930	0.517	0.520455	
q_26		7438	4.572	1.8E-26	***	1930	4.173	3.45E-07	***
q_27		7520	0.857	0.03225		1930	0.855	0.298232	
q_28		7684	1.486	0.000342	*	1930	1.65	0.044582	
q_29	Training	7710	7.579	2.79E-75	***	1930	7.616	1.69E-21	***
q_30		7682	7.867	1.15E-52	***	1930	8.78	5.54E-15	***
q_31	Training	7698	8.187	7.48E-68	***	1930	7.791	4.14E-17	***
q_32	Gaze sensitivity/training	7661	-7.492	1.19E-75	***	1930	-7.702	2.73E-24	***
q_33	Gaze sensitivity/training	7579	-7.637	2.01E-81	***	1930	-8.12	4.24E-27	***
q_34		7578	-1.044	0.009384		1930	-1.554	0.046164	
q_35		7504	-0.08	0.849218		1930	0.457	0.582014	
q_36		7694	-1.197	0.002928		1930	-0.836	0.28726	
q_37	Food motivation	7396	2.603	1.48E-10	***	1930	2.418	0.002101	
q_38		7567	0.36	0.372531		1930	-0.797	0.311813	
q_39		5282	-0.869	0.06455		1930	-1.279	0.104502	
q_40		7186	2.555	1.13E-09	***	1930	2.014	0.012441	
q_41		6276	2.056	1.35E-05	**	1930	1.583	0.052275	
q_42		7389	8.288	6.96E-82	***	1930	6.838	2.96E-15	***
q_43		6566	0.22	0.609657		1930	0.561	0.474122	
q_44		6659	0.359	0.416479		1930	-0.242	0.764603	
q_45		6504	-3.431	1.02E-13	***	1930	-2.858	0.000297	**
q_46		6019	1.411	0.002543		1930	0.195	0.8011	

q_47		7412	1.026	0.014		1930	0.645	0.44821	
q_48		7543	-4.725	1.31E-28	***	1930	-4.327	2.93E-08	***
q_77		7671	5.52	3.76E-34	***	1930	4.922	7.23E-09	***
q_49	Training	2788	-3.943	6.95E-08	***				
q_50	Training	2908	-4.005	8.72E-09	***				
q_51	Training	3027	-1.955	0.007477					
q_52		2356	-2.25	0.00201					
q_53		2359	0.101	0.893644					
q_54		2737	-1.323	0.060491					
q_55		2320	-1.631	0.023645					
q_56		2410	-1.567	0.027623					
q_57		2460	-1.771	0.011546					
q_58		2459	-2.587	0.000372	*				
q_59		2419	-1.769	0.01368					
q_60		2929	-2.054	0.0024					
q_62		2906	-1.824	0.003926					
q_63		2906	-1.786	0.006001					
q_64		2708	-1.679	0.008637					
q_65		2359	-2.234	0.000517					
q_66		2317	-2.161	0.001315					
q_67		2040	-1.813	0.00885					
q_68		2275	-2.108	0.004649					
q_69		2327	-0.18	0.808945					
q_70		2622	-0.31	0.669349					
q_71		1906	-1.557	0.057296					
q_72		2644	-1.729	0.015493					
q_73		2359	-0.356	0.675377					
q_74		2179	-2.758	0.000829					
q_75		2337	-2.795	0.001192					
q_76		2392	-2.222	0.002772					
q_78		2813	-0.607	0.382022					
q_79		2199	-4.15	3.24E-08	***				
q_80		2756	-3.492	2.94E-06	***				
q_81		2315	-2.372	0.001199					
q_82		2469	-2.983	3.48E-05	**				
q_83		2291	-2.338	0.001182					
q_84		2322	2.305	0.001866					
q_85		4013	-0.455	0.410713					
q_86		2187	1.909	0.009671					
q_87		2144	-0.963	0.259549					
q_88		2852	-0.64	0.348517					

q_89		2844	-0.343	0.610356					
q_90		2738	1.419	0.036912					
q_91		2298	0.366	0.612506					
q_92		1375	0.497	0.616438					
q_93		2828	2.152	0.001103					
q_94		2164	0.31	0.687958					
q_95		2239	0.319	0.670421					
q_96		2347	2.634	0.000334	*				
q_97		3161	2.166	0.0006					
q_98		2690	1.162	0.081557					
q_99		3520	3.218	8.48E-08	***				
q_117		4347	-0.788	0.172481					
q_118		2892	0.18	0.78386					
q_124		2363	-0.96	0.178249					
q_125		2372	-1.111	0.123257					
q_129	Training	2204	8.949	2.78E-26	***				
q_130	Training	2001	3.375	1.87E-05	**				
q_131	Training	2118	4.156	1.13E-07	***				
q_132	Training	2169	1.2	0.085922					
q_133	Training	2164	1.968	0.017061					
q_134	Training	2161	2.873	2.46E-05	**				
q_135		1992	0.279	0.783416					
q_136		1956	0.218	0.803499					
q_137		2017	0.559	0.49846					
q_139		1965	0.095	0.932358					
q_140		1982	1.111	0.140465					
q_141		1963	-1.012	0.214433					
q_142		1953	-1.461	0.083072					
q_143		1954	-2.148	0.016169					
q_144		1949	-1.772	0.015797					
q_145		1928	2.521	0.003744					
q_146		1820	0.061	0.938839					
q_148		1904	-2.534	0.003408					
q_149		1892	-0.14	0.881382					
q_150		2122	3.089	4.38E-06	***				
q_151		2086	2.748	0.000108	*				
q_152		1854	1.316	0.103006					
q_154		1555	0.978	0.258983					
q_155		1805	-2.197	0.00578					
q_157	Training	2106	0.662	0.364646					
q_158		1792	-0.821	0.362857					

q_159	Food motivation	1792	-0.982	0.261789					
q_160		1772	0.036	0.964863					
q_161		1482	0.46	0.610167					
q_162		1508	-0.36	0.688071					
q_163	Self control	1448	-4.762	1.05E-07	***				
q_164	Training	2040	1.156	0.110577					
q_168		1242	3.415	0.000403					
q_177	Food motivation	2672	-0.322	0.636127					
q_178	Food motivation	2461	1.913	0.00651					
q_179		2092	0.822	0.304136					
q_180		1802	-4.53	3.76E-08	***				
q_181		1957	0.256	0.756706					
q_187	Food motivation	1788	2.524	0.002877					
q_189		1529	-1.773	0.05092					
q_190		1539	2.026	0.022442					
q_191		1704	0.426	0.632848					
q_193		1484	-0.807	0.376155					
q_194		1556	3.292	0.00024	*				
q_205		2422	-1.679	0.019818					
q_206		2344	-0.899	0.235344					

Appendix H

Statistical Tests from Dognition Memory Task

Appendix **H**: Results of statistical tests from the Chapter 3 analysis of the Dognition memory task. For key to questions, see Appendix A. Results of the exploratory analysis are given on the left and for the conservative analysis on the right. Asterisks represent significance after applying a Bonferroni correction (dividing the significance threshold by 129 for the exploratory analysis and by 30 for the conservative analysis).

Question	**Predictions**	**Exploratory Analysis**				**Conservative Analysis**			
		n	**β**	**p**		**n**	**β**	**p**	
q_20		5044	0.046	0.006488		1386	0.078	0.014894	
q_21		4920	0.053	0.001574		1386	0.077	0.023039	
q_22		4270	0.09	8.15E-07	***	1386	0.11	0.000884	*
q_23		5580	0.095	8.37E-09	***	1386	0.142	3.39E-05	**
q_24		5462	0.163	8.8E-22	***	1386	0.226	1.2E-10	***
q_25		5249	0.099	2.43E-09	***	1386	0.114	0.000742	*
q_26	Memory	5416	0.182	4.66E-26	***	1386	0.311	8.45E-21	***
q_27		5469	0.147	4.21E-20	***	1386	0.188	5.43E-08	***
q_28		5588	0.069	3.46E-05	**	1386	0.14	3.35E-05	**
q_29		5607	0.036	0.036172		1386	0.092	0.007394	
q_30		5582	0.194	6.12E-25	***	1386	0.316	1.24E-14	***
q_31		5597	0.131	3.53E-12	***	1386	0.234	6.68E-10	***
q_32		5576	-0.052	0.001837		1386	-0.092	0.004463	
q_33		5516	-0.026	0.119392		1386	-0.065	0.046309	
q_34		5500	0.068	3.16E-05	**	1386	0.187	1.86E-08	***
q_35		5451	0.042	0.012373		1386	-0.005	0.881904	
q_36		5596	0.044	0.007359		1386	0.021	0.533841	
q_37		5361	0.087	1.01E-07	***	1386	0.133	4.05E-05	**
q_38		5497	0.049	0.0029		1386	0.04	0.221226	
q_39	Memory	3849	0.138	8.02E-13	***	1386	0.138	4.17E-05	**
q_40	Memory	5233	0.145	1.07E-17	***	1386	0.214	3.08E-10	***
q_41	Memory	4555	0.137	2.11E-13	***	1386	0.207	3.52E-10	***
q_42	Memory	5358	0.177	7.05E-23	***	1386	0.265	1.71E-12	***
q_43	Memory	4761	0.036	0.037684		1386	0.048	0.151377	
q_44		4856	0.154	6.85E-19	***	1386	0.182	4.63E-08	***
q_45		4736	-0.021	0.277412		1386	-0.005	0.887271	
q_46		4384	0.145	2.29E-14	***	1386	0.202	5.42E-10	***
q_47	Memory	5372	0.085	2.18E-07	***	1386	0.122	0.000399	*
q_48		5484	-0.067	0.0001	*	1386	-0.043	0.197691	
q_77		5575	0.065	0.000188	*	1386	0.074	0.040473	
q_49		2191	0.02	0.490998					

q_50		2281	0.046	0.097556					
q_51		2370	0.013	0.661088					
q_52		1875	-0.02	0.483721					
q_53		1876	-0.04	0.169911					
q_54		2163	0.165	7.7E-10	***				
q_55		1843	0.033	0.231013					
q_56		1915	0.031	0.252594					
q_57		1951	0.079	0.002992					
q_58		1954	0.052	0.060225					
q_59		1925	0.064	0.019519					
q_60		2310	0.126	1.18E-06	***				
q_62		2292	0.018	0.462773					
q_63		2288	0.05	0.046308					
q_64		2130	0.031	0.218301					
q_65		1873	-0.005	0.821553					
q_66		1836	0.016	0.539057					
q_67		1615	-0.003	0.911842					
q_68		1802	0.053	0.065659					
q_69		1840	-0.011	0.711783					
q_70		2072	-0.067	0.017054					
q_71		1498	-0.006	0.860336					
q_72		2080	-0.041	0.1321					
q_73		1881	-0.066	0.033883					
q_74		1721	-0.066	0.036734					
q_75		1855	-0.082	0.012031					
q_76		1899	-0.055	0.054712					
q_78		2223	0.019	0.477226					
q_79		1747	0.106	0.000163	*				
q_80		2177	-0.021	0.467343					
q_81		1839	0.05	0.078574					
q_82		1966	-0.006	0.818669					
q_83		1821	0.041	0.140627					
q_84		1844	-0.004	0.88969					
q_85		3111	0.021	0.331145					
q_86		1729	-0.013	0.657135					
q_87		1700	-0.028	0.404805					
q_88		2249	0.016	0.54328					
q_89		2244	0.005	0.859397					
q_90		2161	-0.004	0.868595					
q_91		1822	-0.036	0.207979					
q_92		1080	0.127	0.000785					

q_93		2229	0.033	0.199217					
q_94		1718	0.072	0.017592					
q_95		1778	0.003	0.908069					
q_96		1865	0.021	0.459629					
q_97		2473	-0.037	0.129934					
q_98		2102	-0.02	0.441924					
q_99		2743	0.003	0.901419					
q_117		3261	-0.04	0.075226					
q_118		2258	-0.095	0.000201	*				
q_124		1859	0.028	0.328272					
q_125		1870	-0.025	0.364471					
q_129		1746	0.098	0.003416					
q_130		1586	0.102	0.000962					
q_131		1682	0.088	0.004627					
q_132		1725	-0.035	0.166055					
q_133		1719	0.04	0.243229					
q_134		1718	0.061	0.036001					
q_135		1589	-0.022	0.564434					
q_136		1563	-0.013	0.708365					
q_137		1607	-0.048	0.108412					
q_139		1569	0.008	0.845996					
q_140		1580	0.047	0.117722					
q_141		1570	0.005	0.863539					
q_142		1559	-0.01	0.770072					
q_143		1563	0.07	0.057707					
q_144		1559	0.025	0.391602					
q_145		1542	0.09	0.006081					
q_146		1459	-0.102	0.002206					
q_148		1518	-0.045	0.177907					
q_149		1513	0.019	0.608823					
q_150		1683	0.008	0.746986					
q_151		1655	-0.021	0.418486					
q_152		1484	0.009	0.771249					
q_154		1261	0.073	0.031584					
q_155		1443	-0.027	0.389493					
q_157		1670	-0.007	0.795896					
q_158		1435	0.026	0.469401					
q_159		1434	0.117	0.000484					
q_160		1421	-0.098	0.001958					
q_161		1205	0.144	3.02E-05	**				
q_162		1222	-0.005	0.892091					

q_163		1176	-0.038	0.273606					
q_164		1626	0.03	0.285328					
q_168		1011	0.072	0.064366					
q_177		2098	-0.053	0.048869					
q_178		1932	-0.002	0.940863					
q_179		1642	0.063	0.045305					
q_180		1432	-0.058	0.070223					
q_181		1549	0.045	0.160548					
q_187		1428	0.075	0.023562					
q_189		1222	0.124	0.000355	*				
q_190		1231	0.106	0.002288					
q_191		1374	-0.038	0.210268					
q_193		1180	-0.078	0.028446					
q_194		1242	0.008	0.825444					
q_205		1759	-0.079	0.007475					
q_206		1711	-0.064	0.048633					

Appendix I

Statistical Tests from Dognition Memory Versus Pointing Task

Appendix **I**: Results of statistical tests from the Chapter 3 analysis of the Dognition memory versus pointing task. For key to questions, see Appendix A. Results of the exploratory analysis are given on the left and for the conservative analysis on the right. Asterisks represent significance after applying a Bonferroni correction (dividing the significance threshold by 129 for the exploratory analysis and by 30 for the conservative analysis).

Question	**Predictions**	**Exploratory Analysis**				**Conservative Analysis**			
		n	**β**	**p**		**n**	**β**	**p**	
q_20	Communication (emotional)	5653	-0.007	0.555915		1573	0.005	0.809596	
q_21	Communication (emotional)	5509	0.06	1.63E-07	***	1573	0.06	0.007375	
q_22	Communication (emotional)	4769	0.025	0.044576		1573	0.029	0.18413	
q_23	Communication (emotional)	6256	0.004	0.754785		1573	0.019	0.409012	
q_24	Communication (gestural)	6126	-0.036	0.00269		1573	0.008	0.73036	
q_25	Communication	5884	0.048	2.49E-05	**	1573	0.089	9.14E-05	**
q_26	Memory/ Communication (gestural)	6065	-0.053	1.27E-05	**	1573	-0.022	0.337431	
q_27	Communication	6129	0	0.992111		1573	0.034	0.14312	
q_28	Human interest	6262	-0.007	0.568008		1573	0.017	0.448854	
q_29	Human interest	6284	-0.038	0.001304		1573	-0.041	0.075423	
q_30	Communication (verbal)	6258	-0.007	0.610261		1573	-0.024	0.458987	
q_31		6273	-0.039	0.003489		1573	-0.02	0.435816	
q_32		6246	0.004	0.710899		1573	0.004	0.856267	
q_33		6180	0.026	0.023786		1573	0.004	0.868466	
q_34		6164	0.062	2.99E-08	***	1573	0.094	1.83E-05	***
q_35		6112	0.011	0.342341		1573	0.023	0.312124	
q_36		6272	0.043	0.000127	*	1573	0.04	0.069643	
q_37		6015	-0.064	2.9E-08	***	1573	-0.096	2.47E-05	***
q_38		6164	0.113	5.61E-24	***	1573	0.142	1.03E-10	***
q_39	Memory	4304	0.079	1.28E-09	***	1573	0.059	0.008442	
q_40	Memory/ Communication (verbal)	5857	0.004	0.701732		1573	0.019	0.413249	
q_41	Memory	5104	0.051	9.81E-05	*	1573	0.076	0.000859	*
q_42	Memory/ Communication (verbal)	6010	-0.089	2.44E-13	***	1573	-0.001	0.954327	
q_43	Memory	5327	0.057	1.55E-06	***	1573	0.121	3.34E-08	***
q_44		5443	0.049	6.2E-05	**	1573	0.062	0.006936	

q_45		5295	0.075	2.13E-08	***	1573	0.042	0.06778	
q_46	Communication	4922	0.036	0.005094		1573	0.055	0.011685	
q_47	Memory	6020	0.068	2.48E-09	***	1573	0.075	0.001377	*
q_48		6146	0.045	0.000176	*	1573	0.026	0.247082	
q_77		6250	-0.03	0.019899		1573	-0.095	0.000282	**
q_49	Human interest	2372	0.088	1.57E-05	**				
q_50		2475	0.066	0.000548					
q_51	Human interest	2571	0.005	0.814759					
q_52	Human interest	2020	0.005	0.787583					
q_53	Human interest	2021	0	0.988935					
q_54		2342	-0.005	0.810829					
q_55		1983	0.036	0.058248					
q_56		2065	0.048	0.011809					
q_57		2105	0.084	4.79E-06	***				
q_58		2108	0.065	0.000677					
q_59		2075	0.037	0.053427					
q_60		2503	0.016	0.384102					
q_62		2481	0	0.996072					
q_63		2478	-0.014	0.424704					
q_64		2308	-0.003	0.882518					
q_65		2018	-0.027	0.112281					
q_66		1978	-0.031	0.081954					
q_67		1745	-0.012	0.510305					
q_68		1944	-0.01	0.602919					
q_69		1988	0.055	0.007679					
q_70		2240	0.041	0.038844					
q_71		1619	0.158	4.1E-12	***				
q_72		2250	0.061	0.001671					
q_73		2026	0.031	0.162676					
q_74		1857	0.062	0.005447					
q_75		1996	0.031	0.179086					
q_76		2047	0.05	0.012233					
q_78	Human interest	2404	0.051	0.006957					
q_79	Human interest	1879	0.079	5.91E-05	**				
q_80	Human interest	2355	0.051	0.012175					
q_81	Human interest	1983	0.108	4.44E-08	***				
q_82	Human interest	2121	-0.016	0.40446					
q_83		1962	-0.039	0.038986					
q_84	Human interest	1989	-0.053	0.007819					
q_85		3392	0.024	0.109505					
q_86		1867	-0.011	0.58498					

q_87		1836	0.052	0.025273					
q_88		2433	0.022	0.237003					
q_89	Human interest	2428	0.029	0.107525					
q_90		2337	0.017	0.355389					
q_91		1973	0.006	0.737114					
q_92		1163	0.019	0.473104					
q_93		2409	-0.037	0.039073					
q_94		1857	0.057	0.005709					
q_95		1915	-0.002	0.918873					
q_96		2011	-0.013	0.508047					
q_97		2688	-0.022	0.206704					
q_98		2285	-0.029	0.117866					
q_99		2989	-0.068	3.74E-05	**				
q_117		3626	-0.099	1.66E-10	***				
q_118		2472	0.07	0.000133	*				
q_124		2033	0.028	0.157238					
q_125		2041	0.003	0.885399					
q_129		1902	-0.259	7.56E-26	***				
q_130		1729	-0.065	0.002901					
q_131		1834	-0.097	9.97E-06	**				
q_132		1876	-0.059	0.000863					
q_133		1874	-0.022	0.314374					
q_134		1872	-0.056	0.002049					
q_135		1725	-0.063	0.01733					
q_136		1698	0.025	0.322892					
q_137		1744	-0.055	0.008696					
q_139		1702	0.118	3.22E-05	**				
q_140		1713	-0.003	0.89144					
q_141		1702	0.052	0.017983					
q_142		1690	0.093	3.64E-05	**				
q_143		1694	0.11	1.77E-05	**				
q_144		1690	0.078	0.000158	*				
q_145		1671	0.062	0.00769					
q_146		1581	-0.043	0.052029					
q_148		1647	-0.03	0.205853					
q_149		1642	0.007	0.769906					
q_150		1836	-0.166	5.35E-22	***				
q_151		1807	-0.133	9.42E-14	***				
q_152		1608	-0.098	7.58E-06	***				
q_154		1365	-0.034	0.149727					
q_155		1566	-0.02	0.360795					

q_157		1823	-0.073	5.02E-05	**				
q_158		1556	0.019	0.437719					
q_159		1555	-0.117	1.56E-06	***				
q_160		1539	-0.044	0.049171					
q_161		1302	0.039	0.102999					
q_162		1322	-0.019	0.422246					
q_163		1269	-0.011	0.64875					
q_164		1770	-0.189	3.18E-22	***				
q_168		1093	-0.03	0.25198					
q_177		2297	0.083	1.38E-05	**				
q_178		2118	-0.081	4.89E-05	**				
q_179		1803	-0.038	0.093657					
q_180		1565	-0.027	0.228356					
q_181		1691	-0.023	0.319552					
q_187		1555	-0.093	0.000123	*				
q_189		1335	0.042	0.091405					
q_190		1339	0.009	0.701					
q_191		1491	-0.043	0.059314					
q_193	Human interest	1276	0.032	0.203702					
q_194		1338	-0.047	0.060115					
q_205	Human interest	2002	0.091	1.71E-05	**				
q_206		1950	0.012	0.6045					

Appendix J

Statistical Tests from Dognition Memory Versus Smell Task

Appendix **J**: Results of statistical tests from the Chapter 3 analysis of the Dognition memory versus smell task. For key to questions, see Appendix A. Results of the exploratory analysis are given on the left and for the conservative analysis on the right. Asterisks represent significance after applying a Bonferroni correction (dividing the significance threshold by 129 for the exploratory analysis and by 30 for the conservative analysis).

Question	**Predictions**	**Exploratory Analysis**				**Conservative Analysis**			
		n	**β**	**p**		**n**	**β**	**p**	
q_20		5245	-0.03	0.063771		1445	-0.036	0.230351	
q_21		5104	0.004	0.823072		1445	-0.004	0.892576	
q_22		4441	0.003	0.845633		1445	0.01	0.73302	
q_23		5795	-0.007	0.644684		1445	0.014	0.666039	
q_24		5674	-0.06	0.000315	*	1445	-0.039	0.250364	
q_25		5451	0.007	0.678089		1445	-0.016	0.605766	
q_26	Memory	5618	-0.089	1.22E-07	***	1445	-0.089	0.005616	
q_27		5677	-0.001	0.958548		1445	-0.069	0.038234	
q_28		5802	-0.03	0.064549		1445	-0.029	0.367963	
q_29		5822	-0.084	3.33E-07	***	1445	-0.075	0.01736	
q_30		5797	-0.022	0.26104		1445	-0.045	0.305324	
q_31		5811	-0.076	4E-05	**	1445	-0.051	0.157444	
q_32		5787	0.005	0.766448		1445	-0.018	0.55019	
q_33		5724	0.03	0.059268		1445	0.018	0.53901	
q_34		5713	0.055	0.00039		1445	0.144	1.85E-06	***
q_35	Smell	5661	0.099	4.92E-10	***	1445	0.158	2.95E-07	***
q_36	Smell	5811	0.02	0.204402		1445	0.053	0.088716	
q_37		5570	-0.016	0.299938		1445	-0.012	0.706368	
q_38	Hearing	5712	-0.059	0.000167	*	1445	-0.061	0.04377	
q_39	Memory	3992	-0.02	0.278618		1445	0.009	0.7652	
q_40	Memory	5431	-0.131	5.76E-16	***	1445	-0.087	0.005879	
q_41	Memory	4730	-0.002	0.925006		1445	0.009	0.782293	
q_42	Memory	5567	-0.071	2.6E-05	**	1445	-0.015	0.670962	
q_43	Memory	4943	0.07	2.14E-05	**	1445	0.087	0.003865	
q_44		5040	0.021	0.224513		1445	0.054	0.088024	
q_45		4917	0.033	0.071484		1445	0.082	0.012651	
q_46		4554	-0.071	9.36E-05	*	1445	-0.054	0.075704	
q_47	Memory	5581	0.013	0.416351		1445	0.058	0.072229	
q_48		5692	0.023	0.172875		1445	0.029	0.346092	
q_77		5789	0.023	0.189096		1445	0.035	0.302126	
q_49		2253	-0.029	0.271484					

q_50		2348	0.035	0.175799					
q_51		2436	-0.004	0.882204					
q_52		1925	-0.01	0.699048					
q_53		1926	-0.007	0.80523					
q_54		2226	0.055	0.032855					
q_55		1891	0.079	0.002802					
q_56		1965	0.009	0.737726					
q_57		2004	0.049	0.054096					
q_58		2008	0.011	0.677681					
q_59		1975	0.083	0.001424					
q_60		2379	0.023	0.360254					
q_62		2359	0.013	0.58672					
q_63		2355	-0.033	0.160355					
q_64		2193	0.033	0.157353					
q_65		1925	0.032	0.174994					
q_66		1886	0.014	0.579434					
q_67		1662	0.013	0.589614					
q_68		1852	0.003	0.911709					
q_69		1894	0.071	0.011454					
q_70		2130	0.013	0.642291					
q_71		1542	0.051	0.098411					
q_72		2139	0.014	0.601859					
q_73		1931	-0.023	0.454864					
q_74		1768	-0.008	0.789126					
q_75		1904	0.006	0.848389					
q_76		1950	-0.003	0.918651					
q_78		2285	0.082	0.001785					
q_79		1791	0.102	0.000144	*				
q_80		2239	0.013	0.640345					
q_81		1889	-0.019	0.483507					
q_82		2020	0.02	0.447174					
q_83		1869	-0.002	0.925534					
q_84		1894	0.027	0.307755					
q_85		3200	-0.01	0.63006					
q_86		1779	-0.017	0.521501					
q_87		1747	-0.047	0.118882					
q_88		2315	0.067	0.00622					
q_89		2311	0.04	0.099722					
q_90		2224	0	0.995732					
q_91		1875	-0.051	0.058673					
q_92		1105	0.045	0.210765					

q_93		2295	-0.026	0.278547					
q_94		1767	0.04	0.154068					
q_95		1827	0.026	0.329711					
q_96		1915	0.06	0.023601					
q_97		2547	0.006	0.789486					
q_98		2165	0.002	0.929216					
q_99		2826	-0.024	0.296225					
q_117		3383	-0.091	1.7E-05	**				
q_118		2328	0.004	0.873702					
q_124		1916	0.074	0.005884					
q_125		1925	-0.045	0.091838					
q_129		1800	-0.098	0.002515					
q_130		1635	-0.088	0.002985					
q_131		1734	-0.088	0.003224					
q_132	Smell	1777	-0.071	0.002153					
q_133		1773	-0.079	0.004976					
q_134		1772	-0.065	0.00756					
q_135	Hearing	1638	-0.031	0.396788					
q_136		1611	0.042	0.237311					
q_137		1657	-0.049	0.084113					
q_139		1617	0.102	0.006347					
q_140		1629	-0.041	0.136368					
q_141		1617	-0.008	0.782591					
q_142		1606	0.002	0.938155					
q_143		1610	0.052	0.129691					
q_144		1606	0.068	0.015222					
q_145		1588	0.07	0.024545					
q_146		1504	-0.134	2.76E-05	**				
q_148		1565	0.003	0.920363					
q_149		1560	-0.052	0.10804					
q_150		1736	-0.056	0.019953					
q_151		1708	-0.038	0.127599					
q_152		1530	-0.015	0.614037					
q_154		1298	0.037	0.242216					
q_155		1488	-0.049	0.090148					
q_157	Smell	1724	-0.019	0.445456					
q_158		1480	-0.005	0.886187					
q_159		1479	0.007	0.823192					
q_160		1464	-0.122	4.53E-05	**				
q_161		1238	0.035	0.287305					
q_162		1257	-0.011	0.72672					

q_163		1210	-0.011	0.730269					
q_164		1675	-0.086	0.001127					
q_168		1039	0.019	0.598304					
q_177		2165	0.064	0.013718					
q_178		1996	-0.073	0.007106					
q_179		1697	-0.019	0.541007					
q_180		1477	-0.065	0.029816					
q_181		1599	0.063	0.033633					
q_187		1475	-0.035	0.271628					
q_189		1265	0.019	0.57044					
q_190		1268	0.051	0.118054					
q_191		1419	0.022	0.520615					
q_193		1214	0.033	0.325433					
q_194		1276	0.014	0.667798					
q_205		1840	-0.028	0.328656					
q_206		1791	0.061	0.091902					

Appendix K

Statistical Tests from Dognition Inferential Reasoning Task

Appendix **K**: Results of statistical tests from the Chapter 3 analysis of the Dognition inferential reasoning task. For key to questions, see Appendix A. Results of the exploratory analysis are given on the left and for the conservative analysis on the right. Asterisks represent significance after applying a Bonferroni correction (dividing the significance threshold by 129 for the exploratory analysis and by 30 for the conservative analysis).

Question	**Predictions**	**Exploratory Analysis**				**Conservative Analysis**			
		n	**β**	**p**		**n**	**β**	**p**	
q_20		4216	0.044	0.004141		1159	0.044	0.130207	
q_21		4083	0.041	0.008423		1159	0.02	0.521077	
q_22		3557	0.07	2.5E-05	**	1159	0.073	0.014326	
q_23		4645	0.038	0.01322		1159	0.002	0.961048	
q_24		4548	0.053	0.000764		1159	0.043	0.185489	
q_25		4363	0.045	0.003055		1159	0.038	0.206413	
q_26		4510	0.06	0.000193	*	1159	0.061	0.048234	
q_27		4552	0.058	9.09E-05	*	1159	0.037	0.245686	
q_28		4652	0.049	0.001441		1159	0.053	0.081869	
q_29		4668	0.076	1.08E-06	***	1159	0.141	4.34E-06	***
q_30		4645	0.034	0.074875		1159	0.041	0.306219	
q_31		4659	0.079	8.19E-06	**	1159	0.111	0.001275	*
q_32		4644	-0.019	0.2192		1159	-0.043	0.144968	
q_33		4597	-0.016	0.284388		1159	-0.005	0.848339	
q_34		4577	0.008	0.609053		1159	0.019	0.515012	
q_35		4542	-0.065	2.44E-05	**	1159	-0.077	0.010605	
q_36		4659	-0.032	0.033158		1159	0.023	0.451253	
q_37		4457	0.012	0.428044		1159	0.064	0.033414	
q_38		4578	0.02	0.180799		1159	0.056	0.056359	
q_39		3198	0.038	0.030106		1159	0.03	0.314467	
q_40		4352	0.091	3.38E-09	***	1159	0.053	0.083903	
q_41		3806	0.014	0.423027		1159	0.045	0.147122	
q_42		4456	0.057	0.000463		1159	0.036	0.285516	
q_43		3961	0.006	0.709094		1159	0.037	0.211831	
q_44	Reasoning	4030	0.027	0.09877		1159	0.033	0.279095	
q_45	Reasoning	3938	0.043	0.015008		1159	0.07	0.024012	
q_46	Reasoning	3670	0.092	1.16E-07	***	1159	0.068	0.019273	
q_47	Reasoning	4462	0.007	0.665771		1159	0.006	0.859	
q_48	Reasoning	4563	-0.05	0.00165		1159	-0.053	0.074224	
q_77		4640	0.028	0.08724		1159	0.019	0.576374	
q_49		1934	-0.002	0.952565					

q_50		2003	-0.007	0.76278					
q_51		2083	-0.024	0.346696					
q_52		1670	0.004	0.860442					
q_53		1674	0.008	0.772655					
q_54		1914	0.053	0.028925					
q_55		1644	-0.005	0.826608					
q_56		1710	-0.002	0.93076					
q_57		1739	-0.028	0.240191					
q_58		1741	0.009	0.703107					
q_59		1716	-0.032	0.196829					
q_60		2038	0.036	0.11815					
q_62		2019	-0.016	0.4659					
q_63		2017	-0.031	0.163713					
q_64		1873	-0.002	0.914703					
q_65		1667	-0.025	0.242708					
q_66		1635	-0.039	0.081692					
q_67		1439	-0.008	0.725961					
q_68		1599	-0.043	0.087811					
q_69		1633	-0.037	0.155483					
q_70		1833	-0.042	0.101448					
q_71		1332	-0.013	0.654721					
q_72		1843	-0.023	0.367182					
q_73		1678	-0.027	0.336493					
q_74		1531	0.057	0.045685					
q_75		1653	0.016	0.593614					
q_76		1692	0.053	0.039372					
q_78		1963	-0.015	0.533363					
q_79		1556	-0.023	0.364726					
q_80		1925	0.001	0.955947					
q_81		1638	-0.006	0.817047					
q_82		1751	-0.006	0.81669					
q_83		1621	-0.054	0.026817					
q_84		1648	-0.013	0.620249					
q_85		2682	0.055	0.004885					
q_86		1535	0.018	0.467748					
q_87		1518	0.038	0.209816					
q_88		1988	0	0.999105					
q_89		1984	-0.003	0.90281					
q_90		1912	0.004	0.872048					
q_91		1617	0.003	0.907819					
q_92		954	-0.011	0.756569					

q_93		1971	0.037	0.103887					
q_94		1530	0.052	0.048046					
q_95		1581	-0.018	0.483122					
q_96		1663	0.049	0.049494					
q_97		2176	0.012	0.59112					
q_98		1848	0.022	0.340279					
q_99		2399	-0.003	0.901498					
q_117		2737	0.022	0.287964					
q_118		1939	-0.07	0.002503					
q_124		1611	0.024	0.34123					
q_125		1621	0.039	0.119213					
q_129		1513	0.06	0.047413					
q_130		1373	0.099	0.000389					
q_131		1458	0.046	0.096622					
q_132		1492	0.043	0.064907					
q_133		1486	0.03	0.288776					
q_134		1487	0.047	0.051367					
q_135		1378	-0.06	0.110196					
q_136		1352	0.003	0.916521					
q_137		1389	-0.032	0.266122					
q_139		1362	-0.039	0.317864					
q_140		1370	-0.002	0.937201					
q_141		1363	-0.024	0.406471					
q_142		1355	0.008	0.791868					
q_143		1358	-0.006	0.855599					
q_144		1354	0.006	0.814057					
q_145		1338	-0.019	0.524295					
q_146		1267	0.004	0.879208					
q_148		1320	0.013	0.659473					
q_149		1315	0.008	0.79202					
q_150		1458	0.037	0.105153					
q_151		1433	-0.002	0.93394					
q_152		1291	0.032	0.250228					
q_154		1107	0.04	0.181538					
q_155		1252	-0.03	0.282666					
q_157		1447	0.03	0.221073					
q_158		1246	0.003	0.932026					
q_159		1246	-0.002	0.945845					
q_160		1235	0.018	0.533421					
q_161		1059	0.057	0.067284					
q_162		1073	-0.008	0.801402					

q_163		1032	0.006	0.84113					
q_164		1410	0.03	0.228976					
q_168		887	-0.015	0.649467					
q_177		1792	-0.01	0.668904					
q_178		1652	-0.024	0.337989					
q_179		1416	0.043	0.131276					
q_180		1239	0.02	0.483462					
q_181		1341	0.039	0.178225					
q_187		1238	0.024	0.429876					
q_189		1056	0.005	0.871451					
q_190		1069	0.044	0.150762					
q_191		1187	-0.004	0.890522					
q_193		1017	0.006	0.847622					
q_194		1070	0.001	0.972047					
q_205		1382	0.017	0.533973					
q_206		1342	0.01	0.75053					

Appendix L

Statistical Tests from Dognition Physical Reasoning Task

Appendix **L**: Results of statistical tests from the Chapter 3 analysis of the Dognition physical reasoning task. For key to questions, see Appendix A. Results of the exploratory analysis are given on the left and for the conservative analysis on the right. Asterisks represent significance after applying a Bonferroni correction (dividing the significance threshold by 129 for the exploratory analysis and by 30 for the conservative analysis).

Question	**Predictions**	**Exploratory Analysis**				**Conservative Analysis**			
		n	**β**	**p**		**n**	**β**	**p**	
q_20		4076	0.058	0.000252	*	1132	0.061	0.043487	
q_21		3945	0.077	1.37E-06	***	1132	0.101	0.001469	*
q_22		3439	0.076	9.43E-06	**	1132	0.045	0.143385	
q_23		4491	0.026	0.099034		1132	0.044	0.167335	
q_24		4397	0.067	4.29E-05	**	1132	0.149	1.17E-05	***
q_25		4215	0.035	0.024425		1132	0.042	0.182536	
q_26		4360	0.074	7.39E-06	***	1132	0.096	0.002872	
q_27		4396	0.055	0.000366	*	1132	0.058	0.076919	
q_28		4497	0.041	0.009965		1132	0.083	0.008768	
q_29		4512	0.062	0.000127	*	1132	0.101	0.001477	*
q_30		4491	0.054	0.004846		1132	0.049	0.240444	
q_31		4503	0.072	7.39E-05	**	1132	0.07	0.047675	
q_32		4488	-0.033	0.033251		1132	-0.059	0.050564	
q_33		4442	-0.024	0.121074		1132	-0.024	0.422574	
q_34		4426	0.002	0.884079		1132	0.01	0.736052	
q_35		4394	-0.014	0.378887		1132	-0.004	0.897556	
q_36		4506	0.001	0.957703		1132	-0.027	0.390978	
q_37		4307	-0.017	0.29527		1132	0.041	0.192766	
q_38		4426	0.028	0.063555		1132	-0.003	0.911702	
q_39		3098	0.057	0.001719		1132	0.06	0.054509	
q_40		4212	0.067	2.41E-05	**	1132	0.098	0.001981	
q_41		3679	0.042	0.021253		1132	0.06	0.061981	
q_42		4311	0.122	5.02E-13	***	1132	0.128	0.000227	**
q_43		3833	-0.007	0.677569		1132	-0.02	0.519775	
q_44	Reasoning	3893	0.055	0.001203		1132	0.083	0.008622	
q_45	Reasoning	3814	-0.012	0.501049		1132	-0.023	0.482736	
q_46	Reasoning	3545	0.1	2.65E-08	***	1132	0.122	6.21E-05	**
q_47	Reasoning	4315	0.036	0.025607		1132	0.032	0.336278	
q_48	Reasoning	4410	-0.043	0.009323		1132	-0.044	0.151795	
q_77		4486	0.034	0.047294		1132	0.056	0.107524	
q_49		1877	-0.036	0.174178					

q_50		1945	-0.014	0.572794					
q_51		2015	-0.005	0.847585					
q_52		1624	0.011	0.661394					
q_53		1629	0.065	0.016247					
q_54		1861	0.021	0.413248					
q_55		1599	-0.012	0.643297					
q_56		1662	0.015	0.549773					
q_57		1691	0.042	0.089958					
q_58		1692	0.004	0.866369					
q_59		1667	0.025	0.339382					
q_60		1981	0.037	0.118162					
q_62		1962	0.051	0.022278					
q_63		1960	0.033	0.153111					
q_64		1821	0.029	0.184858					
q_65		1619	0.022	0.314278					
q_66		1589	0.022	0.344767					
q_67		1399	0.02	0.401191					
q_68		1553	0.032	0.224856					
q_69		1580	0.007	0.809092					
q_70		1778	0.017	0.517705					
q_71		1295	0.038	0.204658					
q_72		1791	0.02	0.45134					
q_73		1633	-0.056	0.060597					
q_74		1489	0.016	0.582446					
q_75		1607	0.017	0.59553					
q_76		1644	0.003	0.89604					
q_78		1907	0.008	0.754562					
q_79		1511	0.008	0.772142					
q_80		1870	-0.044	0.10558					
q_81		1592	0.034	0.189955					
q_82		1702	0.015	0.564637					
q_83		1577	0.033	0.192215					
q_84		1602	-0.042	0.112518					
q_85		2599	0.032	0.117104					
q_86		1490	-0.023	0.377702					
q_87		1478	0.048	0.131127					
q_88		1932	-0.037	0.132922					
q_89		1928	-0.003	0.895114					
q_90		1858	-0.005	0.839041					
q_91		1575	-0.018	0.491466					
q_92		922	0.035	0.339512					

q_93		1915	-0.01	0.68868					
q_94		1486	0.036	0.192942					
q_95		1535	0.017	0.53046					
q_96		1616	-0.012	0.630165					
q_97		2111	-0.03	0.187918					
q_98		1792	-0.025	0.305415					
q_99		2325	-0.018	0.420656					
q_117		2648	-0.006	0.771052					
q_118		1876	-0.023	0.342505					
q_124		1562	0.033	0.212884					
q_125		1572	0.023	0.381474					
q_129		1469	0.087	0.005919					
q_130		1333	0.078	0.006578					
q_131		1416	0.08	0.005605					
q_132		1449	0.017	0.485688					
q_133		1444	-0.046	0.13079					
q_134		1445	0.016	0.529621					
q_135		1340	-0.016	0.655718					
q_136		1318	-0.017	0.608817					
q_137		1352	0.019	0.515833					
q_139		1326	-0.013	0.752821					
q_140		1334	0.036	0.187247					
q_141		1328	0.013	0.648716					
q_142		1320	-0.028	0.363785					
q_143		1323	-0.042	0.205895					
q_144		1319	0.037	0.1783					
q_145		1304	-0.008	0.809534					
q_146		1234	0.053	0.070774					
q_148		1287	-0.043	0.159164					
q_149		1282	-0.019	0.558798					
q_150		1419	0.051	0.036897					
q_151		1395	0.013	0.605233					
q_152		1258	0.075	0.011343					
q_154		1081	0.108	0.00056					
q_155		1219	0.002	0.945552					
q_157		1408	0.004	0.872905					
q_158		1213	-0.001	0.986046					
q_159		1213	0.027	0.403287					
q_160		1203	-0.021	0.484303					
q_161		1033	0.037	0.254092					
q_162		1047	0	0.990428					

q_163		1006	-0.048	0.137413					
q_164		1371	0.01	0.701952					
q_168		865	-0.005	0.897853					
q_177		1736	0.001	0.976999					
q_178		1600	-0.01	0.71542					
q_179		1373	0.034	0.255376					
q_180		1200	-0.04	0.184555					
q_181		1298	0.068	0.021629					
q_187		1202	0.005	0.868372					
q_189		1028	0.009	0.776785					
q_190		1038	0.076	0.017845					
q_191		1152	-0.061	0.040521					
q_193		982	0.03	0.374082					
q_194		1035	0.004	0.894238					
q_205		1326	-0.011	0.703553					
q_206		1285	-0.037	0.284641					

Appendix M

Statistical Tests from Differential Abundance of the Oral Microbiome by Age

Appendix **M**: Significant results of the MaAsLin2 differential abundance tests from the Chapter 6 analysis of the dog oral microbiome samples in this study as a function of age. All models control for sequencing batch as a random effects variable. Negative *β* values indicate that the feature decreases with age, and positive values indicate that the feature increases with age. The *q* value is the Benjamini-Hochberg FDR correction.

Feature	**β**	**SE**	**n not 0**	**p**	**q**
d__Bacteria.p__Fusobacteriota.c__Fusobacteriia.o__Fusobacteriales.f__Leptotrichiaceae.g__Streptobacillus.s__	-1.76	0.34	27	8.13E-06	0.000219
d__Bacteria.p__Bacteroidota.c__Bacteroidia.o__Flavobacteriales.f__Flavobacteriaceae	-1.43	0.38	32	0.00047	0.00215
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Enterobacterales.f__Pasteurellaceae.g__Frederiksenia.s__	-1.35	0.37	40	0.000689	0.002828
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Enterobacterales.f__Pasteurellaceae	-1.28	0.36	41	0.000835	0.003258
d__Bacteria.p__Fusobacteriota.c__Fusobacteriia.o__Fusobacteriales.f__Leptotrichiaceae.g__Oceanivirga.s__	-1.24	0.45	21	0.008724	0.018366
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Xanthomonadales.f__Xanthomonadaceae.g__Luteimonas.s__	-1.18	0.36	38	0.002118	0.006644
d__Bacteria.p__Bacteroidota.c__Bacteroidia.o__Flavobacteriales.f__Weeksellaceae.g__Bergeyella.s__	-1.17	0.23	42	1.18E-05	0.000219
d__Bacteria.p__Firmicutes.c__Clostridia.o__Oscillospirales.f__Hungateiclostridiaceae.g__Mageeibacillus.s__	-1.14	0.44	18	0.014247	0.027465
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Pseudomonadales.f__Moraxellaceae.g__Psychrobacter.s__	-1.06	0.27	8	0.000383	0.001858
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Burkholderiales.f__Neisseriaceae.g_chiformibius.s__	-1.06	0.3	40	0.001148	0.004137
d__Bacteria.p__Proteobacteria.c__Alphaproteobacteria.o__Rhizobiales.f__Beijerinckiaceae.g__Methylobacterium.Methylorubrum.s__	-0.98	0.28	11	0.001278	0.004259
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Burkholderiales.f__Aquaspirillaceae.g__Aquaspirillum.s__	-0.98	0.37	30	0.010475	0.021216
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Cardiobacteriales.f__Cardiobacteriaceae	-0.95	0.39	14	0.01904	0.034617
d__Bacteria.p__Bacteroidota.c__Bacteroidia.o__Flavobacteriales.f__Weeksellaceae.g__Chryseobacterium.s__	-0.94	0.21	6	4.17E-05	0.000392
d__Bacteria.p__Firmicutes.c__Bacilli.o__Staphylococcales.f__Gemellaceae.g__Gemella.s__	-0.94	0.23	41	0.000188	0.001157
d__Bacteria.p__Fusobacteriota.c__Fusobacteriia.o__Fusobacteriales.f__Leptotrichiaceae.g__Leptotrichia.s__	-0.93	0.36	30	0.012594	0.024877
d__Bacteria.p__Firmicutes.c__Bacilli.o__Lactobacillales.f__Aerococcaceae.g__uncultured.s__	-0.89	0.32	14	0.007481	0.016396
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Enterobacterales	-0.89	0.24	7	0.000512	0.002275
d__Bacteria.p__Proteobacteria.c__Alphaproteobacteria.o__Sphingomonadales.f__Sphingomonadaceae	-0.87	0.27	7	0.002486	0.007333
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Burkholderiales.f__Neisseriaceae	-0.87	0.28	42	0.003357	0.008711
d__Bacteria.p__Firmicutes.c__Bacilli.o__Bacillales.f__Planococcaceae	-0.86	0.2	5	8.79E-05	0.00067

d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Pseudomonadales.f__Moraxellaceae.g__Moraxella.s__	-0.85	0.17	43	1.29E-05	0.000219
d__Bacteria.p__Proteobacteria.c__Alphaproteobacteria.o__Rhizobiales.f__Rhizobiaceae	-0.85	0.19	6	5.75E-05	0.000511
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Cardiobacteriales.f__Cardiobacteriaceae.g__Suttonella.s__	-0.84	0.34	15	0.017226	0.032426
d__Bacteria.p__Proteobacteria.c__Alphaproteobacteria.o__Sphingomonadales.f__Sphingomonadaceae.g__Sphingomonas.s__	-0.83	0.26	7	0.002769	0.007772
d__Bacteria.p__Proteobacteria.c__Alphaproteobacteria.o__Rhizobiales.f__Rhizobiaceae.g__Neorhizobium.s__	-0.81	0.22	5	0.000558	0.002412
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Burkholderiales.f__Alcaligenaceae.g__Pigmentiphaga.s__	-0.8	0.29	9	0.00798	0.017025
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Burkholderiales.f__Burkholderiaceae.g__Lautropia.s__	-0.79	0.25	42	0.003206	0.008549
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Xanthomonadales.f__Xanthomonadaceae.g__Stenotrophomonas.s__	-0.77	0.18	5	0.000156	0.000996
d__Bacteria.p__Actinobacteriota.c__Actinobacteria.o__Propionibacteriales.f__Nocardioidaceae.g__Nocardioides.s__	-0.77	0.19	6	0.000222	0.001184
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Pseudomonadales.f__Moraxellaceae.g__Acinetobacter.s__	-0.75	0.27	8	0.007413	0.016396
d__Bacteria.p__Firmicutes.c__Bacilli.o__Lactobacillales.f__Streptococcaceae.g__Streptococcus.s__	-0.75	0.24	42	0.003064	0.008311
d__Bacteria.p__Proteobacteria.c__Alphaproteobacteria.o__Rhizobiales.f__Beijerinckiaceae.g__Bosea.s__	-0.74	0.21	2	0.001245	0.004239
d__Bacteria.p__Bacteroidota.c__Bacteroidia.o__Sphingobacteriales.f__Sphingobacteriaceae.g__Sphingobacterium.s__	-0.71	0.15	3	3.58E-05	0.000379
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Enterobacterales.f__Pasteurellaceae.g__Pasteurella.s__	-0.7	0.29	41	0.01956	0.034773
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Burkholderiales	-0.69	0.25	7	0.007908	0.017025
d__Bacteria.p__Actinobacteriota.c__Actinobacteria.o__Micrococcales	-0.69	0.19	5	0.000775	0.0031
d__Bacteria.p__Firmicutes.c__Bacilli.o__Mycoplasmatales.f__Mycoplasmataceae.g__Ureaplasma.s__	-0.68	0.37	25	0.076519	0.108346
d__Bacteria.p__Proteobacteria.c__Alphaproteobacteria.o__Rhodobacterales.f__Rhodobacteraceae	-0.68	0.17	5	0.000258	0.00133
d__Bacteria.p__Actinobacteriota.c__Actinobacteria.o__Corynebacteriales.f__Nocardiaceae.g__Rhodococcus.s__	-0.67	0.15	3	6.48E-05	0.000546
d__Bacteria.p__Actinobacteriota.c__Actinobacteria.o__Micrococcales.f__Intrasporangiaceae	-0.67	0.16	2	0.000131	0.000874
d__Bacteria.p__Acidobacteriota.c__Vicinamibacteria.o__Vicinamibacterales.f__uncultured.g__uncultured.s__	-0.67	0.14	2	1.94E-05	0.000239
d__Bacteria.p__Firmicutes.c__Bacilli.o__Erysipelotrichales.f__Erysipelotrichaceae.g__Dielma.s__	-0.66	0.28	13	0.021132	0.036751
d__Bacteria.p__Bacteroidota.c__Bacteroidia.o__Sphingobacteriales.f__Sphingobacteriaceae	-0.66	0.16	3	0.0002	0.001184
d__Bacteria.p__Proteobacteria.c__Alphaproteobacteria.o__Caulobacterales.f__Caulobacteraceae.g__Brevundimonas.s__	-0.65	0.16	4	0.000215	0.001184
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Burkholderiales.f__Neisseriaceae.g__Neisseria.s__	-0.62	0.39	33	0.121517	0.16761
d__Bacteria.p__Proteobacteria.c__Alphaproteobacteria.o__Rickettsiales.f__Mitochondria.g__Mitochondria.s__	-0.61	0.18	4	0.001677	0.005474
d__Bacteria.p__Bacteroidota.c__Bacteroidia	-0.6	0.12	1	7.22E-06	0.000219
d__Bacteria.p__Bacteroidota.c__Bacteroidia.o__Flavobacteriales.f__Flavobacteriaceae.g__Capnocytophaga.s__	-0.59	0.17	43	0.001006	0.003743
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Cardiobacteriales.f__Cardiobacteriaceae.g__Cardiobacterium.s__	-0.57	0.25	7	0.025499	0.041211

d__Bacteria.p__Bacteroidota.c__Bacteroidia.o__Flavobacteriales.f__Flavobacteriaceae.g__Flavobacterium.s__	-0.56	0.35	35	0.11996	0.166901
d__Bacteria.p__Firmicutes.c__Bacilli.o__Erysipelotrichales.f__Erysipelotrichaceae.g__uncultured.s__	-0.55	0.24	12	0.023972	0.039138
d__Bacteria.p__Cyanobacteria.c__Cyanobacteriia.o__Chloroplast.f__Chloroplast.g__Chloroplast.s__	-0.55	0.28	11	0.054537	0.080055
d__Bacteria.p__Firmicutes.c__Bacilli.o__Staphylococcales.f__Staphylococcaceae.g__Jeotgalicoccus.s__	-0.52	0.18	4	0.006807	0.015785
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria	-0.5	0.12	0	0.000212	0.001184
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Pseudomonadales.f__Pseudomonadaceae.g__Pseudomonas.s__	-0.49	0.23	6	0.038482	0.060364
d__Bacteria.p__Proteobacteria.c__Alphaproteobacteria.o__Rhizobiales.f__Devosiaceae.g__Devosia.s__	-0.47	0.14	1	0.002228	0.006856
d__Bacteria.p__Proteobacteria.c__Alphaproteobacteria.o__Rhizobiales.f__Beijerinckiaceae.g__Microvirga.s__	-0.45	0.22	4	0.042269	0.065661
d__Bacteria.p__Firmicutes.c__Bacilli.o__Lactobacillales.f__Aerococcaceae.g__Abiotrophia.s__	-0.43	0.28	41	0.124244	0.169907
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Burkholderiales.f__Comamonadaceae	-0.39	0.29	39	0.187519	0.247959
d__Bacteria.p__Bacteroidota.c__Bacteroidia.o__Bacteroidales.f__Prevotellaceae.g__Prevotella_7.s__	-0.39	0.16	3	0.020603	0.036225
d__Bacteria.p__Firmicutes.c__Bacilli.o__Erysipelotrichales.f__Erysipelotrichaceae.g__Solobacterium.s__	-0.32	0.17	2	0.060401	0.087857
d__Bacteria.p__Firmicutes.c__Clostridia	-0.3	0.12	1	0.019542	0.034773
d__Bacteria.p__Firmicutes.c__Negativicutes.o__Veillonellales.Selenomonadales.f__Veillonellaceae.g__Veillonella.s__	-0.3	0.19	2	0.132038	0.179035
d__Bacteria.p__Synergistota.c__Synergistia.o__Synergistales.f__Synergistaceae.g__Candidatus_Tammella.s__	0.22	0.12	2	0.065993	0.094276
d__Bacteria.p__Actinobacteriota.c__Actinobacteria.o__Actinomycetales.f__Actinomycetaceae.g__Actinomyces.s__	0.32	0.21	41	0.145319	0.193758
d__Bacteria.p__Firmicutes.c__Clostridia.o__Peptostreptococcales.Tissierellales.f__Family_XI.g__Peptoniphilus.s__	0.32	0.16	1	0.050712	0.078018
d__Bacteria.p__Spirochaetota.c__MVP.15.o__MVP.15.f__MVP.15.g__MVP.15.s__	0.34	0.13	2	0.013439	0.026223
d__Bacteria.p__Bacteroidota.c__Bacteroidia.o__Bacteroidales.f__Prevotellaceae.g__Prevotellaceae_UCG.003.s__	0.39	0.24	5	0.112743	0.158236
d__Bacteria.p__Bacteroidota.c__Bacteroidia.o__Bacteroidales.f__Prevotellaceae	0.4	0.2	4	0.053131	0.079695
d__Bacteria.p__Bacteroidota.c__Bacteroidia.o__Bacteroidales	0.44	0.29	12	0.135313	0.181933
d__Bacteria.p__Firmicutes.c__Bacilli.o__Lactobacillales.f__Aerococcaceae	0.44	0.19	4	0.021877	0.037237
d__Bacteria.p__Firmicutes.c__Clostridia.o__Peptostreptococcales.Tissierellales.f__Family_XI.g__W5053.s__	0.48	0.2	5	0.022658	0.037764
d__Bacteria.p__Firmicutes.c__Clostridia.o__Oscillospirales.f__Hungateiclostridiaceae	0.5	0.25	9	0.053296	0.079695
d__Bacteria.p__Bacteroidota.c__Bacteroidia.o__Bacteroidales.f__F082.g__F082.s__	0.5	0.17	3	0.004875	0.011818
d__Bacteria.p__Firmicutes.c__Clostridia.o__Peptostreptococcales.Tissierellales.f__Anaerovoracaceae.g__Family_XIII_UCG.001.s__	0.5	0.14	5	0.00119	0.004137
d__Bacteria.p__Fusobacteriota.c__Fusobacteriia.o__Fusobacteriales.f__Leptotrichiaceae	0.51	0.21	4	0.023028	0.037984
d__Bacteria.p__Firmicutes.c__Clostridia.o__Clostridia_vadinBB60_group.f__Clostridia_vadinBB60_group.g__Clostridia_vadinBB60_group.s__	0.51	0.16	4	0.003065	0.008311
d__Bacteria.p__Bacteroidota.c__Bacteroidia.o__Bacteroidales.f__Porphyromonadaceae	0.54	0.21	7	0.015716	0.029936

d__Bacteria.p__Bacteroidota.c__Bacteroidia.o__Bacteroidales.f__Dysgonomonadaceae.g__Proteiniphilum.s__	0.55	0.23	12	0.02178	0.037237
d__Bacteria.p__Patescibacteria.c__Gracilibacteria.o__Absconditabacteriales_.SR1..f__Absconditabacteriales_.SR1..g__Absconditabacteriales_.SR1..s__	0.58	0.3	40	0.064425	0.092865
d__Bacteria.p__Firmicutes.c__Bacilli.o__Erysipelotrichales.f__Erysipelotrichaceae.g__.Anaerorhabdus._furcosa_group.s__	0.62	0.25	27	0.017561	0.032507
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Pseudomonadales.f__Moraxellaceae	0.64	0.32	38	0.052241	0.079606
d__Bacteria.p__Patescibacteria.c__Saccharimonadia.o__Saccharimonadales.f__Saccharimonadaceae.g__Candidatus_Saccharimonas.s__	0.66	0.3	12	0.033419	0.052941
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Xanthomonadales	0.66	0.33	17	0.054502	0.080055
d__Bacteria.p__Patescibacteria.c__Saccharimonadia.o__Saccharimonadales.f__Saccharimonadaceae.g__TM7x.s__	0.66	0.23	23	0.006	0.014329
d__Bacteria.p__Bacteroidota.c__Bacteroidia.o__Bacteroidales.f__Paludibacteraceae	0.71	0.26	17	0.010312	0.021152
d__Bacteria.p__Bacteroidota.c__Bacteroidia.o__Bacteroidales.f__Bacteroidales.g__Bacteroidales.s__	0.71	0.16	3	8.3E-05	0.000664
d__Bacteria.p__Firmicutes.c__Clostridia.o__Peptostreptococcales.Tissierellales.f__Peptostreptococcaceae.g__Peptostreptococcus.s__	0.73	0.32	12	0.028457	0.045531
d__Bacteria.p__Bacteroidota.c__Kapabacteria.o__Kapabacteriales.f__Kapabacteriales.g__Kapabacteriales.s__	0.73	0.26	28	0.006355	0.014953
d__Bacteria.p__Firmicutes.c__Bacilli.o__Izemoplasmatales.f__Izemoplasmatales.g__Izemoplasmatales.s__	0.76	0.15	5	1.37E-05	0.000219
d__Bacteria.p__Campylobacterota.c__Campylobacteria.o__Campylobacterales.f__Rs.M59_termite_group.g__Rs.M59_termite_group.s__	0.76	0.19	6	0.00028	0.001399
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Burkholderiales.f__Rhodocyclaceae.g__Propionivibrio.s__	0.78	0.25	16	0.003376	0.008711
d__Bacteria.p__Firmicutes.c__Clostridia.o__Peptostreptococcales.Tissierellales.f__Anaerovoracaceae.g__.Eubacterium._brachy_group.s__	0.78	0.28	14	0.009025	0.018754
d__Bacteria.p__Firmicutes.c__Clostridia.o__Peptostreptococcales.Tissierellales.f__Fusibacteraceae.g__Fusibacter.s__	0.8	0.3	39	0.010764	0.021528
d__Bacteria.p__Bacteroidota.c__Bacteroidia.o__Bacteroidales.f__Marinifilaceae.g__Odoribacter.s__	0.81	0.17	4	1.77E-05	0.000239
d__Archaea.p__Euryarchaeota.c__Methanobacteria.o__Methanobacteriales.f__Methanobacteriaceae.g__Methanobrevibacter.s__	0.82	0.19	4	9.98E-05	0.000694
d__Bacteria.p__Firmicutes.c__Clostridia.o__Oscillospirales.f__Oscillospiraceae	0.82	0.26	9	0.002521	0.007333
d__Bacteria.p__Firmicutes.c__Clostridia.o__Lachnospirales.f__Lachnospiraceae.g__Johnsonella.s__	0.83	0.27	31	0.004386	0.010965
d__Bacteria.p__Firmicutes.c__Negativicutes.o__Veillonellales.Selenomonadales.f__Selenomonadaceae.g__Selenomonas.s__	0.84	0.24	12	0.001189	0.004137
d__Bacteria.p__Actinobacteriota.c__Actinobacteria.o__Corynebacteriales.f__Corynebacteriaceae	0.85	0.3	16	0.007058	0.016089
d__Bacteria.p__Bacteroidota.c__Bacteroidia.o__Bacteroidales.f__MgMjR.022.g__MgMjR.022.s__	0.86	0.35	14	0.017676	0.032507
d__Bacteria.p__Firmicutes.c__Bacilli.o__RF39.f__RF39.g__RF39.s__	0.88	0.28	13	0.002594	0.007412
d__Bacteria.p__Desulfobacterota.c__Desulfovibrionia.o__Desulfovibrionales.f__Desulfomicrobiaceae.g__Desulfomicrobium.s__	0.89	0.38	25	0.022656	0.037764
d__Bacteria.p__Firmicutes.c__Clostridia.o__Peptostreptococcales.Tissierellales.f__Family_XI	0.9	0.23	8	0.000424	0.001997

d__Bacteria.p__Bacteroidota.c__Bacteroidia.o__Bacteroidales.f__Tannerellaceae.g__Tannerella.s__	0.94	0.28	31	0.001816	0.005811
d__Bacteria.p__Bacteroidota.c__Bacteroidia.o__Bacteroidales.f__Paludibacteraceae.g__uncultured.s__	1	0.2	11	1.11E-05	0.000219
d__Bacteria.p__Firmicutes.c__Clostridia.o__Peptostreptococcales.Tissierellales.f__Peptostreptococcaceae.g__Filifactor.s__	1.03	0.34	29	0.004578	0.011269
d__Bacteria.p__Spirochaetota.c__Spirochaetia.o__Spirochaetales.f__Spirochaetaceae	1.08	0.23	16	2.45E-05	0.00028
d__Bacteria.p__Campylobacterota.c__Campylobacteria.o__Campylobacterales.f__Arcobacteraceae.g__Arcobacter.s__	1.09	0.39	25	0.00714	0.016089
d__Bacteria.p__Desulfobacterota.c__Desulfovibrionia.o__Desulfovibrionales.f__Desulfoplanaceae.g__Desulfoplanes.s__	1.12	0.35	19	0.002489	0.007333
d__Bacteria.p__Firmicutes.c__Clostridia.o__Peptostreptococcales.Tissierellales.f__Peptostreptococcaceae.g__uncultured.s__	1.16	0.38	34	0.003694	0.009383
d__Bacteria.p__Spirochaetota.c__Spirochaetia.o__Spirochaetales.f__Spirochaetaceae.g__Treponema.s__	1.19	0.33	38	0.000925	0.003524
d__Bacteria.p__Firmicutes.c__Clostridia.o__Peptostreptococcales.Tissierellales.f__Family_XI.g__Helcococcus.s__	1.21	0.33	21	0.000663	0.002791
d__Bacteria.p__Bacteroidota.c__Bacteroidia.o__Bacteroidales.f__Rikenellaceae.g__Rikenellaceae_RC9_gut_group.s__	1.23	0.22	13	1.71E-06	0.000137
d__Bacteria.p__Firmicutes.c__Bacilli.o__Acholeplasmatales.f__Acholeplasmataceae.g__Acholeplasma.s__	1.23	0.29	31	9.92E-05	0.000694
d__Bacteria.p__Firmicutes.c__Clostridia.o__Peptostreptococcales.Tissierellales.f__Anaerovoracaceae	1.34	0.28	12	1.94E-05	0.000239
d__Bacteria.p__Synergistota.c__Synergistia.o__Synergistales.f__Synergistaceae.g__Fretibacterium.s__	1.41	0.3	27	3.79E-05	0.000379
d__Bacteria.p__Desulfobacterota.c__Desulfovibrionia.o__Desulfovibrionales.f__Desulfovibrionaceae.g__Desulfovibrio.s__	1.48	0.27	18	2.9E-06	0.000155
d__Bacteria.p__Firmicutes.c__Clostridia.o__Christensenellales.f__Christensenellaceae.g__Christensenellaceae_R.7_group.s__	1.64	0.33	17	1.34E-05	0.000219
d__Bacteria.p__Chloroflexi.c__Anaerolineae.o__Anaerolineales.f__Anaerolineaceae.g__Flexilinea.s__	1.66	0.25	16	7.48E-08	1.2E-05

Appendix N

Statistical Tests from Differential Abundance of the Oral Microbiome by Host Species

Appendix **N**: Significant results of the MaAsLin2 differential abundance tests from the Chapter 6 analysis of the canid oral microbiome samples from this study and Podar et al. (2024) as a function of host species. All models control for study as a random effects variable. Negative *β* values indicate that the feature is more common in dogs, and positive values indicate that the feature is more common in wolves. The *q* value is the Benjamini-Hochberg FDR correction.

Feature	**β**	**SE**	**n not 0**	**p**	**q**
d__Bacteria.p__Spirochaetota.c__Spirochaetia.o__Spirochaetales.f__Spirochaetaceae.g__Treponema	-3.23	0.7	57	2.79E-05	0.00041
d__Bacteria.p__Patescibacteria.c__Gracilibacteria.o__Absconditabacteriales_.SR1..f__Absconditabacteriales_.SR1..g__Absconditabacteriales_.SR1.	-3.08	0.6	61	1.95E-05	0.00037
d__Bacteria.p__Synergistota.c__Synergistia.o__Synergistales.f__Synergistaceae.g__Fretibacterium	-2.86	0.7	43	0.000156	0.001391
d__Bacteria.p__Bacteroidota.c__Bacteroidia.o__Bacteroidales.f__Prevotellaceae.g__Alloprevotella	-2.63	0.61	64	5.5E-05	0.000628
d__Bacteria.p__Bacteroidota.c__Bacteroidia.o__Flavobacteriales.f__Flavobacteriaceae.__	-2.54	0.71	41	0.019851	0.081439
d__Bacteria.p__Bacteroidota.c__Kapabacteria.o__Kapabacteriales.f__Kapabacteriales.g__Kapabacteriales	-2.49	0.54	46	2.08E-05	0.00037
d__Bacteria.p__Bacteroidota.c__Bacteroidia.o__Bacteroidales.f__Rikenellaceae.g__Rikenellaceae_RC9_gut_group	-2.35	0.58	27	0.000114	0.001141
d__Bacteria.p__Firmicutes.c__Clostridia.o__Christensenellales.f__Christensenellaceae.g__Christensenellaceae_R.7_group	-2.33	0.76	32	0.003311	0.01766
d__Bacteria.p__Bacteroidota.c__Bacteroidia.o__Bacteroidales.f__Porphyromonadaceae.g__Porphyromonas	-2.09	0.3	74	1.55E-09	8.25E-08
d__Bacteria.p__Desulfobacterota.c__Desulfovibrionia.o__Desulfovibrionales.f__Desulfovibrionaceae.__	-2.01	0.36	12	3.85E-07	1.31E-05
d__Bacteria.p__Chloroflexi.c__Anaerolineae.o__Anaerolineales.f__Anaerolineaceae.g__Flexilinea	-1.94	0.7	28	0.007549	0.036604
d__Bacteria.p__Firmicutes.c__Bacilli.o__Erysipelotrichales.f__Erysipelotrichaceae.__	-1.91	0.46	24	0.000105	0.001124
d__Bacteria.p__Fusobacteriota.c__Fusobacteriia.o__Fusobacteriales.f__Fusobacteriaceae.g__Fusobacterium	-1.57	0.45	72	0.000778	0.005124
d__Bacteria.p__Patescibacteria.c__Dojkabacteria.o__Dojkabacteria.f__Dojkabacteria.g__Dojkabacteria	-1.56	0.35	10	3.15E-05	0.00042
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Pseudomonadales.f__Moraxellaceae.__	-1.54	0.69	57	0.028204	0.106089
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Enterobacterales.f__Pasteurellaceae.g__Frederiksenia	-1.46	0.86	63	0.093202	0.24382
d__Bacteria.p__Firmicutes.c__Clostridia.o__Peptostreptococcales.Tissierellales.f__Family_XI.g__Helcococcus	-1.4	0.6	33	0.056298	0.169957
d__Bacteria.p__Bacteroidota.c__Bacteroidia.o__Bacteroidales.f__Tannerellaceae.g__Tannerella	-1.37	0.52	52	0.039505	0.134484
d__Bacteria.p__Desulfobacterota.c__Desulfovibrionia.o__Desulfovibrionales.f__Desulfomicrobiaceae.g__Desulfomicrobium	-1.31	0.73	48	0.085144	0.239
d__Bacteria.p__Patescibacteria.c__Microgenomatia.o__Candidatus_Pacebacteria.f__Candidatus_Pacebacteria.g__Candidatus_Pacebacteria	-1.16	0.32	8	0.000581	0.004039

d__Bacteria.p__Firmicutes.c__Bacilli.o__Acholeplasmatales.f__Acholeplasmataceae.g__Acholeplasma	-1.15	0.64	39	0.073937	0.215089
d__Bacteria.p__Firmicutes.c__Clostridia.o__Peptostreptococcales.Tissierellales.f__Peptostreptococcaceae.g__uncultured	-1.14	0.66	62	0.088096	0.243024
d__Bacteria.p__Bacteroidota.c__Bacteroidia.o__Bacteroidales.f__F082.g__F082	-1.11	0.49	9	0.027222	0.106089
d__Bacteria.p__Firmicutes.c__Clostridia.o__Oscillospirales.f__Oscillospiraceae.__	-1.11	0.59	17	0.065817	0.195012
d__Bacteria.p__Firmicutes.c__Clostridia.o__Peptostreptococcales.Tissierellales.__.__	-1.1	0.34	23	0.001699	0.010067
d__Bacteria.p__Patescibacteria.c__Parcubacteria.o__Candidatus_Moranbacteria.f__Candidatus_Moranbacteria.g__Candidatus_Moranbacteria	-1.06	0.42	8	0.014124	0.062165
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Pseudomonadales.__.__	-1.05	0.38	10	0.007435	0.036604
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Burkholderiales.f__Comamonadaceae.g__Corticibacter	-1	0.58	65	0.089895	0.243225
d__Bacteria.p__Firmicutes.c__Bacilli.o__Lactobacillales.__.__	-1	0.4	15	0.014764	0.062165
d__Bacteria.p__Firmicutes.c__Bacilli.o__Erysipelotrichales.f__Erysipelotrichaceae.g__Erysipelothrix	-0.97	0.49	11	0.051947	0.163355
d__Bacteria.p__Desulfobacterota.c__Desulfobulbia.o__Desulfobulbales.f__Desulfobulbaceae.g__Desulfobulbus	-0.96	0.43	9	0.026836	0.106089
d__Bacteria.p__Firmicutes.c__Bacilli.o__RF39.f__RF39.g__RF39	-0.96	0.56	20	0.09448	0.24382
d__Bacteria.p__Patescibacteria.c__Gracilibacteria.o__JGI_0000069.P22.f__JGI_0000069.P22.g__JGI_0000069.P22	-0.95	0.55	53	0.091209	0.243225
d__Bacteria.p__Firmicutes.c__Clostridia.o__Peptostreptococcales.Tissierellales.f__Family_XI.g__W5053	-0.94	0.47	11	0.050508	0.163355
d__Bacteria.p__Firmicutes.c__Clostridia.o__Oscillospirales.__.__	-0.93	0.28	9	0.001282	0.007889
d__Bacteria.p__Bacteroidota.c__Bacteroidia.o__Bacteroidales.f__Paludibacteraceae.__	-0.93	0.51	26	0.076915	0.219758
d__Bacteria.p__Firmicutes.c__Clostridia.o__Lachnospirales.f__Defluviitaleaceae.g__Defluviitaleaceae_UCG.011	-0.81	0.4	72	0.052069	0.163355
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Xanthomonadales.f__Rhodanobacteraceae.__	-0.77	0.35	7	0.030129	0.109561
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Burkholderiales.f__Comamonadaceae.g__Brachymonas	0.82	0.37	7	0.028512	0.106089
d__Bacteria.p__Actinobacteriota.c__Actinobacteria.o__Micrococcales.f__Micrococcaceae.__	1.03	0.38	7	0.008333	0.038093
d__Bacteria.p__Actinobacteriota.c__Actinobacteria.o__Propionibacteriales.f__Propionibacteriaceae.__	1.03	0.38	28	0.007816	0.036783
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Burkholderiales.f__Comamonadaceae.__	1.31	0.61	65	0.035738	0.124305
d__Bacteria.p__Actinobacteriota.c__Actinobacteria.o__Micrococcales.__.__	1.4	0.47	36	0.003623	0.0187
d__Bacteria.p__Fusobacteriota.c__Fusobacteriia.o__Fusobacteriales.f__Leptotrichiaceae.g__Leptotrichia	1.47	0.75	48	0.054965	0.169122
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Enterobacterales.f__Pasteurellaceae.__	1.61	0.81	64	0.051992	0.163355
d__Bacteria.p__Firmicutes.c__Clostridia.o__Peptostreptococcales.Tissierellales.f__Peptostreptococcaceae.__	1.61	0.3	31	1.05E-06	2.79E-05
d__Bacteria.p__Actinobacteriota.c__Actinobacteria.o__Actinomycetales.f__Actinomycetaceae.g__Actinomyces	1.62	0.42	72	0.000218	0.001742
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Burkholderiales.f__Neisseriaceae.g__Neisseria	1.69	0.68	62	0.014632	0.062165
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Enterobacterales.f__Pasteurellaceae.g__uncultured	1.71	0.53	24	0.001788	0.010216

d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Burkholderiales.f__Neisseriaceae.g_chiformibius	1.72	0.78	65	0.031424	0.111729
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Burkholderiales.f__Burkholderiaceae.g__Lautropia	1.89	0.6	66	0.002337	0.012893
d__Bacteria.p__Actinobacteriota.c__Actinobacteria.o__Euzebyales.f__Euzebyaceae.g__uncultured	1.91	0.42	73	3.78E-05	0.000465
d__Bacteria.p__Actinobacteriota.c__Actinobacteria.o__Corynebacteriales.__.__	1.96	0.5	10	0.000211	0.001742
d__Bacteria.p__Firmicutes.c__Bacilli.o__Lactobacillales.f__Aerococcaceae.g__Abiotrophia	2.15	0.61	57	0.000801	0.005124
d__Bacteria.p__Firmicutes.c__Clostridia.o__Peptostreptococcales.Tissierellales.f__Peptostreptococcaceae.g__Proteocatella	2.28	0.51	63	2.82E-05	0.00041
d__Bacteria.p__Firmicutes.c__Bacilli.o__Lactobacillales.f__Streptococcaceae.g__Streptococcus	2.35	0.62	66	0.000312	0.002266
d__Bacteria.p__Firmicutes.c__Clostridia.o__Peptostreptococcales.Tissierellales.f__Family_XI.g__Parvimonas	2.47	0.63	43	0.000229	0.001742
d__Bacteria.p__Firmicutes.c__Bacilli.o__Staphylococcales.f__Gemellaceae.g__Gemella	2.52	0.63	61	0.00014	0.001317
d__Bacteria.p__Actinobacteriota.c__Actinobacteria.o__Corynebacteriales.f__Corynebacteriaceae.g__Corynebacterium	3.04	0.55	70	4.1E-07	1.31E-05
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Pseudomonadales.f__Moraxellaceae.g__Acinetobacter	3.09	0.63	15	5.9E-06	0.000135
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Pseudomonadales.f__Pseudomonadaceae.g__Pseudomonas	3.51	0.48	16	2.54E-10	2.03E-08
d__Bacteria.p__Firmicutes.c__Clostridia.o__Clostridiales.f__Clostridiaceae.__	5.9	0.45	16	1.04E-20	1.67E-18

Appendix O

Statistical Tests from Differential Abundance of the Gut Microbiome by Host Species

Appendix **O**: Significant results of the MaAsLin2 differential abundance tests from the Chapter 6 analysis of the canid gut microbiome samples from this study, Reese et al. (2021), and Xu et al. (2021) as a function of host species. All models control for study as a random effects variable. Negative *β* values indicate that the feature is more common in dogs, and positive values indicate that the feature is more common in wolves. The *q* value is the Benjamini-Hochberg FDR correction.

Feature	**β**	**SE**	**n not 0**	**p**	**q**
d__Bacteria.p__Firmicutes.c__Bacilli.o__Lactobacillales.f__Lactobacillaceae.g__HT002	-5.51	0.62	24	1.68E-12	2.85E-10
d__Bacteria.p__Firmicutes.c__Bacilli.o__Lactobacillales.f__Lactobacillaceae.g__Lactobacillus	-4.95	0.65	26	2.85E-10	1.82E-08
d__Bacteria.p__Firmicutes.c__Bacilli.o__Lactobacillales.f__Lactobacillaceae.__	-4.73	0.68	19	2.73E-09	1.15E-07
d__Bacteria.p__Firmicutes.c__Bacilli.o__Lactobacillales.f__Lactobacillaceae.g__Ligilactobacillus	-4.36	0.64	26	5.37E-09	1.82E-07
d__Bacteria.p__Firmicutes.c__Bacilli.o__Erysipelotrichales.f__Erysipelotrichaceae.g__Turicibacter	-3.88	0.52	36	2.46E-08	5.93E-07
d__Bacteria.p__Firmicutes.c__Bacilli.o__Erysipelotrichales.f__Erysipelotrichaceae.g__Holdemanella	-3.83	0.6	30	3.02E-08	6.37E-07
d__Bacteria.p__Firmicutes.c__Bacilli.o__Erysipelotrichales.f__Erysipelatoclostridiaceae.g__Erysipelatoclostridium	-3.07	0.41	33	3.22E-10	1.82E-08
d__Bacteria.p__Firmicutes.c__Clostridia.o__Peptostreptococcales.Tissierellales.f__Peptostreptococcaceae.g__Romboutsia	-2.26	0.6	53	0.000415	0.003745
d__Bacteria.p__Firmicutes.c__Clostridia.o__Oscillospirales.f__Ruminococcaceae.g__Faecalibacterium	-2.16	0.7	40	0.003166	0.019112
d__Bacteria.p__Firmicutes.c__Bacilli.o__Lactobacillales.f__Streptococcaceae.g__Streptococcus	-2.07	0.67	45	0.003015	0.018874
d__Bacteria.p__Firmicutes.c__Bacilli.o__Lactobacillales.__.__	-1.99	0.44	19	2.98E-05	0.000388
d__Bacteria.p__Firmicutes.c__Clostridia.o__Clostridia_UCG.014.f__Clostridia_UCG.014.g__Clostridia_UCG.014	-1.44	0.44	40	0.001656	0.012171
d__Bacteria.p__Firmicutes.c__Clostridia.o__Clostridiales.f__Clostridiaceae.g__Sarcina	-1.26	0.49	11	0.012036	0.054974
d__Bacteria.p__Bacteroidota.c__Bacteroidia.o__Bacteroidales.f__Prevotellaceae.g__Prevotella_9	-1.15	0.48	27	0.021035	0.081858
d__Bacteria.p__Firmicutes.c__Bacilli.o__Erysipelotrichales.f__Erysipelatoclostridiaceae.g__Erysipelotrichaceae_UCG.003	-1.14	0.48	22	0.022277	0.083663
d__Bacteria.p__Firmicutes.c__Clostridia.o__Oscillospirales.f__Ruminococcaceae.g__Fournierella	-1.01	0.37	26	0.007521	0.036504
d__Bacteria.p__Firmicutes.c__Clostridia.o__Peptostreptococcales.Tissierellales.f__Peptostreptococcaceae.g__Terrisporobacter	-0.99	0.53	37	0.06515	0.183507
d__Bacteria.p__Firmicutes.c__Clostridia.o__Lachnospirales.f__Lachnospiraceae.g__Tyzzerella	-0.91	0.46	24	0.053457	0.158495
d__Bacteria.p__Firmicutes.c__Clostridia.o__Oscillospirales.f__Butyricicoccaceae.__	-0.87	0.39	34	0.028894	0.097661
d__Bacteria.p__Firmicutes.c__Clostridia.o__Clostridiales.f__Clostridiaceae.g__Candidatus_Arthromitus	-0.74	0.36	17	0.042185	0.132023
d__Bacteria.p__Actinobacteriota.c__Actinobacteria.o__Corynebacteriales.f__Corynebacteriaceae.__	-0.69	0.35	14	0.050636	0.152811

d__Bacteria.p__Firmicutes.c__Clostridia.o__Oscillospirales.f__Ruminococcaceae.g__Anaerofilum	-0.58	0.33	8	0.085876	0.230367
d__Bacteria.p__Proteobacteria.c__Alphaproteobacteria.o__Rhodobacterales.f__Rhodobacteraceae.__	0.46	0.19	3	0.019056	0.078547
d__Bacteria.p__Actinobacteriota.c__Actinobacteria.o__Corynebacteriales.f__Dietziaceae.g__Dietzia	0.47	0.25	8	0.058372	0.170085
d__Bacteria.p__Actinobacteriota.c__Actinobacteria.o__Corynebacteriales.f__Nocardiaceae.g__Rhodococcus	0.51	0.26	10	0.059448	0.170284
d__Bacteria.p__Firmicutes.c__Bacilli.o__Lactobacillales.f__Enterococcaceae.g__Enterococcus	0.52	0.3	17	0.084698	0.230367
d__Bacteria.p__Bacteroidota.c__Bacteroidia.o__Flavobacteriales.f__Weeksellaceae.__	0.54	0.24	6	0.030535	0.101186
d__Bacteria.p__Firmicutes.c__Clostridia.o__Lachnospirales.f__Lachnospiraceae.g__GCA.900066575	0.56	0.24	9	0.025653	0.092241
d__Bacteria.p__Actinobacteriota.c__Actinobacteria.o__Propionibacteriales.f__Nocardioidaceae.g__Nocardioides	0.58	0.2	6	0.007544	0.036504
d__Bacteria.p__Firmicutes.c__Clostridia.o__Clostridia_vadinBB60_group.f__Clostridia_vadinBB60_group.g__Clostridia_vadinBB60_group	0.61	0.35	7	0.090112	0.237952
d__Bacteria.p__Firmicutes.c__Clostridia.o__Clostridiales.__.__	0.63	0.19	2	0.001936	0.013632
d__Bacteria.p__Firmicutes.c__Clostridia.o__Peptostreptococcales.Tissierellales.f__Anaerovoracaceae.__	0.68	0.21	5	0.002408	0.016275
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Enterobacterales.f__Enterobacteriaceae.__	0.75	0.36	16	0.03934	0.125444
d__Bacteria.p__Firmicutes.c__Bacilli.o__Bacillales.f__Planococcaceae.g__Sporosarcina	0.8	0.36	11	0.028497	0.097661
d__Bacteria.p__Firmicutes.c__Clostridia.o__Peptostreptococcales.Tissierellales.f__Anaerovoracaceae.g__Family_XIII_AD3011_group	0.81	0.27	6	0.004654	0.025726
d__Bacteria.p__Firmicutes.c__Clostridia.o__Christensenellales.f__Christensenellaceae.g__Christensenellaceae_R.7_group	0.81	0.36	16	0.027715	0.097582
d__Bacteria.p__Actinobacteriota.c__Coriobacteriia.o__Coriobacteriales.f__Eggerthellaceae.__	0.82	0.21	5	0.000304	0.003214
d__Bacteria.p__Actinobacteriota.c__Actinobacteria.o__Micrococcales.f__Micrococcaceae.__	0.82	0.32	12	0.013799	0.059795
d__Bacteria.p__Firmicutes.c__Bacilli.__.__.__	0.83	0.35	11	0.023996	0.08816
d__Bacteria.p__Actinobacteriota.c__Coriobacteriia.o__Coriobacteriales.f__Eggerthellaceae.g__Parvibacter	0.83	0.34	16	0.016904	0.071419
d__Bacteria.p__Firmicutes.c__Clostridia.o__Oscillospirales.f__Ruminococcaceae.g__Phocea	0.88	0.17	4	1.44E-06	2.7E-05
d__Bacteria.p__Firmicutes.c__Bacilli.o__Bacillales.__.__	0.94	0.32	9	0.005883	0.031068
d__Bacteria.p__Firmicutes.c__Negativicutes.o__Acidaminococcales.f__Acidaminococcaceae.g__Phascolarctobacterium	0.97	0.53	47	0.074937	0.207613
d__Bacteria.p__Firmicutes.c__Clostridia.o__Lachnospirales.f__Lachnospiraceae.g__.Eubacterium._hallii_group	0.98	0.34	13	0.00756	0.036504
d__Bacteria.p__Firmicutes.c__Bacilli.o__Erysipelotrichales.f__Erysipelatoclostridiaceae.__	0.98	0.45	22	0.0324	0.105301
d__Bacteria.p__Bacteroidota.c__Bacteroidia.o__Bacteroidales.f__Tannerellaceae.g__Parabacteroides	1.02	0.49	24	0.045214	0.13893
d__Bacteria.p__Campylobacterota.c__Campylobacteria.o__Campylobacterales.f__Campylobacteraceae.g__Campylobacter	1.09	0.46	19	0.021161	0.081858
d__Bacteria.p__Firmicutes.c__Clostridia.o__Clostridiales.f__Clostridiaceae.g__Clostridium_sensu_stricto_7	1.19	0.46	13	0.011644	0.05466
d__Bacteria.p__Actinobacteriota.c__Actinobacteria.o__Micrococcales.f__Intrasporangiaceae.__	1.27	0.25	9	3.94E-06	6.06E-05
d__Bacteria.p__Bacteroidota.c__Bacteroidia.o__Bacteroidales.f__Marinifilaceae.g__Odoribacter	1.27	0.33	8	0.000421	0.003745

d__Bacteria.p__Firmicutes.c__Clostridia.o__Clostridiales.f__Clostridiaceae.g__Hathewaya	1.32	0.39	9	0.001397	0.011246
d__Bacteria.p__Proteobacteria.c__Gammaproteobacteria.o__Enterobacterales.f__Enterobacteriaceae.g__Escherichia.Shigella	1.41	0.6	40	0.021312	0.081858
d__Bacteria.p__Firmicutes.c__Clostridia.o__Clostridiales.f__Clostridiaceae.g__Clostridium_sensu_stricto_4	1.47	0.4	11	0.000462	0.003902
d__Bacteria.p__Firmicutes.c__Bacilli.o__Erysipelotrichales.f__Erysipelotrichaceae.__	1.52	0.6	38	0.013576	0.059795
d__Bacteria.p__Firmicutes.c__Clostridia.o__Oscillospirales.f__Oscillospiraceae.g__UCG.005	1.54	0.52	45	0.004719	0.025726
d__Bacteria.p__Bacteroidota.c__Bacteroidia.o__Bacteroidales.f__Bacteroidaceae.g__Bacteroides	1.54	0.51	61	0.00383	0.022317
d__Bacteria.p__Firmicutes.c__Bacilli.o__Erysipelotrichales.f__Erysipelotrichaceae.g__Catenisphaera	1.79	0.42	33	7.2E-05	0.000811
d__Bacteria.p__Firmicutes.c__Clostridia.o__Peptostreptococcales.Tissierellales.f__Peptostreptococcaceae.g__Paeniclostridium	1.8	0.57	38	0.002671	0.017359
d__Bacteria.p__Bacteroidota.c__Bacteroidia.o__Bacteroidales.f__Prevotellaceae.g__Alloprevotella	1.96	0.59	57	0.001507	0.011576
d__Bacteria.p__Bacteroidota.c__Bacteroidia.o__Bacteroidales.__.__	1.99	0.51	21	0.000406	0.003745
d__Bacteria.p__Fusobacteriota.c__Fusobacteriia.o__Fusobacteriales.f__Fusobacteriaceae.g__Fusobacterium	2	0.45	61	3.84E-05	0.000464
d__Bacteria.p__Firmicutes.c__Clostridia.o__Lachnospirales.f__Lachnospiraceae.g__Oribacterium	2.05	0.4	22	3.24E-06	5.47E-05
d__Bacteria.p__Firmicutes.c__Clostridia.o__Lachnospirales.f__Lachnospiraceae.g__.Ruminococcus._torques_group	2.48	0.36	59	1.33E-08	3.75E-07
d__Bacteria.p__Fusobacteriota.c__Fusobacteriia.o__Fusobacteriales.f__Fusobacteriaceae.__	3	0.64	52	1.74E-05	0.000246

VITA

Kyle Cristofer Marcusson Smith

Education

2019-2025	Ph.D.	Pennsylvania State University
2019-2022	M.A.	Pennsylvania State University
2012-2016	B.S.	Duke University

Employment

2022-2025	Instructor	Pennsylvania State University
2020-2022	Teaching Assistant	Pennsylvania State University
2017-2019	Lab Manager	Duke Canine Cognition Center
2012-2016	Tour Guide	Duke Lemur Center

Publications

2023 Salomons, H., **Smith, K.C.M.**, Callahan-Beckel, M., Callahan, M., Levy, K., Kennedy, B.S., Bray, E.E., Gnanadesikan, G.E., Horschler, D.J., Gruen, M., Tan, J., White, P., vonHoldt, B.M., MacLean, E.L., and B. Hare. Response to Hansen Wheat et al.: Additional analysis further supports the early emergence of cooperative communication in dogs compared to wolves raised with more human exposure. *Learning & Behavior 51*, 131-134.

2021 Salomons, H., **Smith, K.C.M.**, Callahan-Beckel, M., Callahan, M., Levy, K., Kennedy, B.S., Bray, E.E., Gnanadesikan, G.E., Horschler, D.J., Gruen, M., Tan, J., White, P., vonHoldt, B.M., MacLean, E.L., and B. Hare. Cooperative communication with humans evolved to emerge early in domestic dogs. *Current Biology 31*(14), 3137-3144.e11