OUR CANINE CONNECTION: THE HISTORY, BENEFITS AND FUTURE OF HUMAN-DOG INTERACTIONS

EDITED BY: Sandra McCune, Aubrey Howard Fine, Eric G. Strauss and Evan MacLean

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OUR CANINE CONNECTION: THE HISTORY, BENEFITS AND FUTURE OF HUMAN-DOG INTERACTIONS

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EDITORIAL
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Editorial: Our Canine Connection: The History, Benefits and Future of Human-Dog Interactions

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Editorial on the Research Topic

Our Canine Connection: The History, Benefits and Future of Human-Dog Interactions

We are current witness to profound changes in the demography and social behavior of humans that includes paradigm shifts in science, religion and philosophy. Coupled with the profound impacts of plant and animal domestication, the modern forces of urbanization and technological transformation have created complex social communities yoked to the ecology and behavior of domestic animals whose roles were likely unimagined only a century ago. Scholars refer to the changing place of humanity on the planet and have named the current epoch the Anthropocene, but it would not have been possible without agricultural and animal domestication that dates back to antiquity. Our efforts to better understand the lives of working domestic animals have great potential to enhance the processes through which these animals are bred, selected, trained, and cared for, resulting in a more benevolent ecosystem for this mutual relationship. In this series, we present a suite of papers that aim to sharpen our understanding of the origins, behavior, cognition and welfare of the domestic dog, and apply these considerations to their working roles in society. The goal of this exercise is to provide a review of the science to date and suggest new frameworks for future use-inspired research in the canine sciences.

The genesis of this project was made possible and funded by the Annenberg PetSpace Foundation through the establishment of a Leadership Institute (https://www.annenbergpetspace.org/about/leadership). The Institute seeks to foster and support the understanding of the human-animal bond through research and program implementation. Fellowships are awarded by the Foundation in order to bring together experts with diverse backgrounds for intellectual exchange and visioning for future research. The first two rounds of the Fellowship Program focused on canine research and its applications. Each round included a multi-day retreat which served as an intellectual salon, with an open agenda for the exchange of ideas. The first retreat was held in 2017 (https://www.annenbergpetspace.org/about/leadership) and spanned a universe of expertise from history, genetics and evolution, to behavior, welfare and human social dynamics. Emerging from this effort was a single multi-author paper (1) that argued for carving out a space for canine science and the domestic dog in the context of tackling the declining environmental conditions of the globe. Titled *Humanity's Best Friend*, the team of authors considered the role of domestication and the complex relationship that we have with domestic dogs as tools to better achieve Sustainable Development Goals (SDG) as outlined by the United Nations.

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Building on the success of this project, the Annenberg PetSpace Foundation hosted a second round of Leadership Fellows in 2020 (https://www.annenbergpetspace.org/about/leadership). The strategy employed at this retreat was to narrow the focus to the specific dimensions of working dogs, human animal interaction (HAI) research and implications for the understanding of domestication as a tool for both improving human health outcomes and those of our canine companions. What follows is the suite of 12 papers authored by select members of both retreats and their colleagues. The papers are organized into five broad categories, which we explore below.

EVOLUTION AND BEHAVIOR (THREE PAPERS)

Three papers address the issues of dog domestication, overall ecological character and genetics. Serpell tackles the controversial and dynamic story of the domestication of dogs from their wolf ancestors. Serpell compares the evidence for two predominant origin stories. The first suggests a commensal relationship of wolves exploiting food scraps from humans that gradually gave rise to a full-blown mutualism of collaborative hunting, resource protection and social companionship. The second model, which Serpell favors, suggests an active role for Paleolithic peoples who actively captured wolf pups as a form of pet-keeping, otherwise known as the cross-species adoption hypothesis. Serpell suggests that the ecologies of both species make such a phenomenon quite plausible.

Wynne picks up the domestication saga much later in time and explores the complex relationships humans have had with domestic dogs in recent history. Unlike theories that suggest that dogs are more compliant than wolves and therefore more likely to be domesticated, Wynne argues that the foraging nature of dogs facilitates a strong independence, unbounded by the complex social order of wolves. Along with this set of traits comes the ability of humans and dogs to interact across species boundaries, with Wynne characterizing the nature of this relationship as one of "super-dominance," with allusion to Tinbergen's ethological concept of supernormal stimuli. The third contribution to this set of papers comes from the lab of Elinor Karlsson and is led by Chen et al. They argue for the implementation of modern tools of genomics to better understand the nature of dogs in general and specifically genetic potential for diverse working applications. They argue for the application of statistical genomic approaches as a way to revolutionize the field of working dogs leading to a much higher degree of success in selection and training of puppies. Featured is a step-by-step guide for breeders to implement estimated breeding values in their programs through genotyping and DNA sequencing.

TRAINING (2 PAPERS)

Two papers address issues regarding the training and selection of dogs for working roles. Hall et al. leads a team that reviews current practices in working dog training concluding that many of the techniques used today predate major advances in our understanding of dog cognition, many of which have occurred in the last two decades. The authors identify specific areas in which working dog training should be modernized for the Twenty-first century, and identify key research questions which have yet to be explored.

Bray et al. collaborates with a team to identify practices through which the selection and performance of working dogs can be optimized. They point out that while dogs provide very complex services in their roles as working animals, the processes by which they are selected and trained have numerous points of failure, which collectively are expensive and burdensome to trainers and stakeholders, and have potential negative implications for dog welfare and human health The authors stress the need to develop new selection criteria at the level of the individual candidate animal and to enhance breeding and rearing practices at the population level, in order to best serve working dogs and the humans they assist.

HUMAN HEALTH (3 PAPERS)

Three papers explore the positive effects that working and companion dogs have on human health, with an emphasis on the impact of these relationships on the dogs as well. McCune and Promislow consider the arc of aging in humans and dogs, which differ considerably due to their variation in lifespans. This apparent disequilibrium actually provides a myriad of opportunities for a deeper understanding of the aging process and the mutual companionship opportunities that exist because of it. Using the World Health Organization's *Healthy Aging Initiative*, the authors explore the research on aging of both dogs and humans and how we can better understand and support this process through innovative research and program development.

Gee et al., along with Kerri Rodriguez use a biopsychosocial framework to contextualize current research on the contribution of human-animal interactions to human wellbeing. The authors also focus on a wide range of social contexts in which dogs have been involved in adjunct or complementary therapy to a diverse community of people in need. The authors provide a framework for analysis and help set an agenda for further research in this transdisciplinary field.

Finally, Barker and Gee consider the state of knowledge in the use of therapy dogs in formal hospital settings. The goal here is to maximize the benefit to human patients while also protecting the physical and mental health of the dogs. As they note, this places human medicine and the veterinary sciences in a collaborative partnership that currently lacks the appropriate understanding and policies to ensure success in all dimensions. The paper presents a clear rationale for canine-assisted interventions in a hospital setting and explores the challenges presented by these novel therapies. A two-decade program in a medical center is used as an exemplar along with a thorough analysis of the research in order to build the case for future expansion of these practices.

ANIMAL WELFARE (2 PAPERS)

Two of the papers in this series deal directly with the welfare of working dogs and also the consideration of the world from the dog's perspective. Cobb et al. review papers on working dogs from the last decade (2011–2020) with an emphasis on human interaction, ethics and the five domains of animal welfare. As the awareness of, and research on animal welfare has increased, the authors use this growing body of research to evaluate past practices and current challenges for developing a sustainable and responsible model in which working dogs are embraced as co-workers.

Horowitz evaluates dog-human interaction under the umbrella of HAI research from the perspective of the welfare of the dog as the "silent partner." In reviewing the literature, she poses fundamental questions about the appropriateness of dogs in research, the impact on the species and individuals, even developing a model for a dog's agency in research. She poses the idea that dogs should have a system of providing "consent" for participation, similar to what we expect from human research studies.

IMPROVING RESEARCH AND LOOKING FORWARD (2 PAPERS)

Two of the papers have a focus on research methodologies and future challenges and opportunities of domestic canine science. Rodriguez et al. seek to improve the quality of future research by looking at the strengths and weaknesses of current methodologies. They investigate ways in which experimental design can be improved in order to sharpen the hypotheses that are being investigated and strengthen the conclusions that can be drawn from this work. These challenges are particularly acute with a species as cosmopolitan as the domestic dog. The onus on improving the research is an issue that has dogged the wild canid research community as well, especially with respect to managing coyotes (2). The convergence of concern in domestic and wild canid research suggests supplying a new standard to the research effort can amplify the effectiveness of the work and reduce the risk of implementing weak inferences from the findings.

The final paper from the MacLean et al. serves as a synthesis and prospectus that unifies the suite of papers and looks toward the future of use-inspired research in the field of anthrozoology. Focusing on a range of topics, relevant to stakeholders, funders and the research community, the authors delineate a path forward for this interdisciplinary work. Drawing on similar disciplines that investigate human-dominated natural systems and synanthropic species, such as urban ecology, we argue that HAI can have profound implications on human wellbeing and that of our canine partners. The collection of articles will provide a comprehensive synthesis of the current trends within the field. We hope you enjoy the series and find it relevant to your work and a catalyst to your aspirations.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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CONCEPTUAL ANALYSIS
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Variability in Human-Animal Interaction Research

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The field of Human-Animal Interaction (HAI) is plagued with mixed results. Some findings appear to indicate that interacting with a companion animal is beneficial for some aspect of human health and well-being, while other research outcomes are inconclusive or even indicate the opposite. The purpose of this paper is to take a closer look at this variability in research outcomes and to provide plausible explanations and potential remedies. Some of the reasons for mixed results are likely due to the wide variety of methodologies implemented, intermittent use of standardized measures and manualized protocols, variability in human and animal participants, and limited quantification of human-animal interactions or definitions of pet ownership. Variability in research outcomes is not unique to HAI and is, in fact, not uncommon in many more established fields such as psychology and medicine. However, the potential reasons for the variability may be linked to the unique nature of HAI in that, in its' simplest form, it involves two complex organisms, a human and an animal, interacting in dynamic ways. We argue that this complexity makes research in this field particularly challenging and requires a broad spectrum of theoretical and methodological considerations to improve rigor while ensuring the validity and reliability of conclusions drawn from study results.

Keywords: human-animal interaction (HAI), methodology, animal-assisted intervention (AAI), variability in outcomes, replication

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INTRODUCTION

The idea that interacting with companion animals conveys health and well-being benefits to humans goes back for centuries. Empirical research on the impact of pets on people, however, dates to the 1980s (1). Among the most influential early investigations were studies reporting that pet owners had significantly lower rates of mortality following heart attacks (2) and that interacting with dogs produced decreases in blood pressure and levels of physiological stress (3). Over the last 20 years, research on the health and therapeutic implications of the human-animal bond, including animal-assisted interventions (AAI), has grown exponentially. Hundreds of papers on these topics are now published in academic journals each year, and centers devoted to the study of human-animal relationships have been established in North America, Europe, Asia, and Australia. In addition, nearly 50 educational institutions now offer undergraduate or graduate degrees in human-animal relationships (4).

In recent years, the notion that pet owners are healthier and happier than non-pet owners has gained popularity. A 2016 survey by the Human-Animal Bond Research Institute (HABRI) found that 71% of pet owners were aware of research showing that pets improve human mental

and physical health. Another HABRI survey found that 97% of family doctors who responded agreed there are health benefits of owning pets. There is a mismatch, however, between the results of empirical investigations and public perceptions of the positive effects of companion on human health and well-being (5). Some studies have found, for example, that pet owners have lower rates of mortality and obesity, higher self-esteem, are happier, and have decreased blood pressure and stress levels (6). Yet other studies have found no differences in these measures. Further, some researchers have reported that pet owners are more likely to suffer from disorders such as anxiety, insomnia, depression, obesity, ulcers, and panic attacks (6).

Research on pet ownership and loneliness exemplifies variations in results of studies on the impact of living with pets on well-being. Gilbey and Tani (7) reviewed 13 studies published between 1986 and 2014 comparing levels of loneliness in pet-owners and non-owners. Using standardized psychological instruments, five of the studies found that pet owners were less lonely, seven found no differences in the degree of loneliness in owners and non-owners, and one study reported mixed results (7). Further, only one of eight studies published between 2014 and 2020 found that pet owners were less lonely (8). Four of these studies reported no difference between the groups, and two produced mixed results. When the older and newer studies are combined, six reported beneficial associations between loneliness and pet ownership, while twelve found no association between pet-ownership and loneliness.

Outcomes from studies on the efficacy of animal-assisted intervention for improving human health and well-being have also not been uniformly positive, with similarly mixed results. For example, several studies have suggested that therapy dog visits may have beneficial physiological and psychological effects on hospitalized pediatric patients (9, 10). However, in one of the largest multi-site randomized controlled trials (RCT) on the effects of therapy dog visits on pediatric patients to date, researchers found that children in outpatient cancer treatment units who received 4 months of weekly therapy dog visits did not exhibit reduced stress, reduced anxiety, or improved quality of life compared to children randomized to treatment as usual (11). Reviews of the literature have pointed out significant threats to construct validity regarding the therapeutic value of the physical animal in AAI (12) as well as the potential for inflated false positives in findings (13) that may contribute to mixed findings in the field.

Variations in Research Results Are Common in Science

The high degree of variation found in the results of HAI research is also common in more established fields. Experimental psychology in particular has been plagued with conflicting findings. A 2015 article in Science reported the results of replication attempts of 100 studies published in three reputable psychology journals (14). Only 39% of the results of the original studies could be replicated. Indeed, the results of widely accepted findings in behavioral research have been called into question by inconsistent findings. These include the impact of nasal oxytocin administration on interpersonal trust (15), changes in female mate preferences associated with ovulation (16), and the ego-depletion model of self-control (17).

Variability in outcomes is also common in clinical medicine. For example, a recent review of studies published in three leading medical journals found that standard treatments were based on the results of nearly 400 randomized controlled trials that failed to replicate (18). Among these were hormone therapies for menopause, breast cancer screening, knee surgery, and CPR techniques. A search of the phrase "variability in outcomes" in PubMed returned 195,828 hits, with 74,977 hits when restricted to the most recent 5-year period. The published manuscripts from these searches covered a wide range of topics such as the longitudinal course of posttraumatic stress disorder [PTSD; (19)], treatment of polycystic kidney disease (20), and recovery from arthroscopic anterior shoulder repair (21), to name but a few.

Concern for persistent variation in research results across science (the "replication crisis") was sparked by a 2005 paper by John Ioannidis titled, "Why Most Published Research Findings Are False." Ioannidis argued that inconsistent and false findings are particularly common in research areas that have several characteristics. These include small sample sizes, small effect sizes, "flexibility in designs, definitions, and outcomes" and, finally, fields that suddenly become "hot" (22). These problems are characteristic of many HAI research studies. Take, for example, a recent meta-analysis of research on the efficacy of animal-assisted psychotherapy for the treatment of trauma. The researchers found that seven of the nine clinical trials in the analysis were statistically underpowered; five of them had fewer than 17 subjects (23). A meta-analysis of eleven reports on the efficacy of prison-based dog programs found that most of the treatment effects in these studies were low [average $d = 0.15$; (24)]. Finally, HAI falls into Ioannides' "hot field" category. According to a Google Scholar search using the term "therapy dog," the annual number of published papers related to canine-assisted therapies jumped from 60 in 2010 to 237 in 2019.

VARIABILITY IN METHODS AND MEASUREMENT IN HAI RESEARCH

A specific consideration in explaining outcome variance in HAI research is that studies significantly vary in their methodological design and rigor. HAI researchers use a wide variety of designs to answer comparable questions in the field, ranging from case studies, single-subject research, and qualitative interviews to observational, cross-sectional, and longitudinal studies. While early studies in HAI were largely limited by a lack of control conditions and small sample sizes, more recent studies have substantially improved in their methodological rigor (25). Despite recent advances in methodology, systematic reviews of both animal-assisted intervention and pet ownership studies repeatedly state that is difficult to draw definitive conclusions from the data due methodological weaknesses across studies [e.g., (26, 27)].

An emerging number of studies using randomized clinical trial designs have shown promise in legitimizing the validity and

strength of evidence in the field. However, even conclusions from RCTs can be limited by a high risk of bias from inadequate concealment and blinding [e.g., (28)]. Even the most rigorous studies can also vary widely in their control or comparison conditions. For example, intervention studies may feature no control at all, an active control (e.g., interaction with toys or stuffed animals), or a no-treatment control (e.g., waitlist or withdrawal periods). With a variety of control and comparison conditions used in the field, this leads to both variability in outcomes as well as difficulty making cross-study comparisons. In a systematic review of eight RCTs evaluating the effects of AAI on psychosocial outcomes, several different comparison conditions were identified including treatment without an animal present, active comparisons with human visitation or quiet reading, and waitlist controls (29). The type of control condition used may have direct impacts in study results. For example, a moderator analysis conducted as part of a meta-analysis on the effects of AAI in medical settings found that studies with a social control condition (i.e., featuring human interaction but not animal interaction) had significantly smaller effect sizes than studies with a non-social control condition (30).

Additionally, there is widespread variability in measurement methods in HAI. Specifically, the use of standardized, validated measures to quantify outcomes has been inconsistent across HAI research (25). In a systematic review of 48 studies assessing AAI in the form of reading to therapy dogs among school-aged children, only 13 studies used standardized measures with established validity and reliability to measure outcomes (31). Rather, many studies incorporate subjective ratings, researcher-created measures, or modified existing measures which makes it difficult to compare findings across studies. Still, among studies that do incorporate standardized measures, the sheer number of measures available to quantify the constructs of interest to HAI research (i.e., mental health, social functioning, quality of life) has resulted in further variability in the literature. For example, a systematic review of 14 studies on the efficacy of AAI for children with autism found that no two studies used the same standardized assessment tool (32). This lack of replication of measurement across studies prevents the ability to make informed conclusions with meta-analytic methods, which is crucial for providing an evidence base for the field (33).

Standardized measures also vary in the appropriateness of content for the theoretical outcomes of HAI. For example, a popular scale of loneliness called the UCLA Loneliness Scale was recently evaluated for its appropriateness to quantify beneficial social effects of pet ownership (34). Both qualitative and quantitative evaluation suggested that only 6/20 items were likely sensitive to change following pet ownership or pet acquisition, concluding that despite its widespread use the scale lacks efficacy for quantifying the effect of pets on loneliness. Therefore, while the use of consistent measures across studies is important for replication purposes, measures must be chosen for their sensitivity to change following animal interaction.

VARIABILITY IN HUMAN PARTICIPANTS IN HAI RESEARCH

When quantifying the role that animals play in our lives, it is important to consider the heterogeneity in how humans may perceive, respond to, and interact with animals. Individual differences in demographic variables such as age, gender, and race/ethnicity may contribute significantly to outcome variance. For example, a meta-analysis of outcomes from AAT found that studies of young children had the most consistently positive outcomes, while other age groups exhibited more variability in outcomes (35). Not only may males and females have different hormonal responses to interaction with animals (36), but females have been found to report more positive behaviors and attitudes toward animals (37) and toward animal-assisted interventions in general (38). While these gender differences in attitudes and responses may not be unique to HAI, equal care should be taken to consider gender-specific effects in analyses as in other fields of research. Ethnicity, cultural, and religious differences may also contribute to attitudes and perceptions of animals (39, 40), However, neither demographic variables nor other potentially confounding variables such as marital status, sources of social support, and socioeconomic status are consistently controlled for in HAI studies (41). The omission of key explanatory variables in analyses can lead to invalid conclusions if unmeasured confounding variables are partially or fully explaining significant findings. For example, a recent systematic review of the impact that pets have on child and adolescent development found that 14 of 22 studies did not consider any confounding variables in analyses, leading authors to conclude that no firm conclusions can be drawn from the literature (42). In addition to controlling for these confounders, future large-scale research studies should also consider the extent to which demographic or contextual variables may mediate outcomes (43). Mediator and/or sub-group analyses may also aid in understanding for whom and under what conditions individuals benefit from HAI (5, 44).

In addition to demographic and environmental variables, human participants in HAI research often vary widely in their physical and mental health. As a key research question in this field is understanding how animal interaction may benefit individuals of sensitive populations, HAI research often includes a range of disabilities, disorders, and chronic conditions. Frequently, participants are selected for participation in research based on a single diagnosis (e.g., posttraumatic stress disorder, cerebral palsy, etc.). However, not only is there variation across studies in how and when this diagnosis was made, there can also be considerable phenotypic variation among individuals with the same condition (e.g., autism spectrum disorder, ASD). In a systematic review of 13 studies addressing the impact of AAI on social behaviors of children with ASD, nine different terms were used to describe participants' diagnosis and/or severity including autism spectrum disorder, autism, autistic disorder, moderate autism, early childhood autism, and atypical autism (45). Thus, it is difficult to compare results across these studies when participants' symptoms and behavioral profiles are markedly

different. Even in phenotypically similar disorders, there is also often participant variability in severity, progressiveness, and duration of the condition or disability. However, these factors are often not controlled for or considered in statistical analyses. For example, a systematic review of the effects of AAI on individuals with dementia found that only 13 of 32 studies controlled for the severity of dementia in their design or analysis (26). Disability severity and progressiveness can be important explanatory variables in psychosocial outcomes such as quality of life, however. In a 2006 study of the psychosocial effects of mobility service dogs for their handlers, having a progressive condition (e.g., muscular dystrophy, multiple sclerosis) was an important moderator of whether having a service dog was associated with higher positive affect (46).

Emerging research also suggests that human genetic differences may play a key role in the study of human-animal interactions. A recent 2019 study indicated that there may be a genetic and heritable component for choosing to have a pet (47). Specifically, researchers examined pet dog ownership among over 35,000 pairs of twins in Sweden and found that more than 50% of the variability in whether an individual owned a dog at the time of the study was explained by genetics. Although the specific genes associated with dog ownership could not be identified, this research suggests that a combination of environmental and genetic influences could influence an individual's affinity toward animals. Genetic variability is also an important consideration in research incorporating hormones and/or neuropeptides such as oxytocin and cortisol. Variations in the oxytocin receptor gene have been associated with human attachment behavior (48) and caregiving styles (49), and recently have been demonstrated to be associated with dog-owner attachment (50). Similarly, there are many sources of genetic and environmental influence on cortisol synthesis, metabolism, and reactivity (51, 52).

Finally, it is also important to consider differences in human experiences, thoughts, and behavior that may contribute to variable outcomes from HAI. Research suggests that interactions and relationships with companion animals can be impacted by human personality traits (53, 54). In addition, human attachment styles (e.g., avoidant or anxious attachment) can be important in understanding variation in the human-animal bond. For example, studies have shown that pet owners with avoidant attachment to their pets experience less stress-reducing benefits from their pets (55) and report negative expectations about a pet's availability and responsiveness (56). Quality and quantity of previous animal interaction, which is often unaccounted for in HAI research (5), is another important aspect of inter-participant variability. Future HAI research should be mindful of these differing experiences, including previous and current pet ownership as well as any fears or aversions toward animals, in both the design and analysis of studies.

VARIABILITY IN ANIMAL PARTICIPANTS IN HAI RESEARCH

Not only is there unique variation in human participants that needs to be accounted for, but also in animal participants. Animals' temperament, personality, training, and even physiology are becoming increasingly important considerations in understanding variability in HAI research. Of course, there is wide variability in the species of animals studied in this field (e.g., mammals, birds, exotics, farm animals) that contributes to heterogeneity across studies (57). However, even within a single species, there is also variability in animals' appearance, disposition, rearing/training, and history of human interaction that may influence outcomes (58). As the animal itself is a key component of HAI, detailed descriptions and considerations of animal characteristics are critical to disentangling potential mechanisms of benefits (12). In the case of AAI, a consideration of animals' varying qualities also parallels the increasing acceptance of animals as individual agents rather than tools or objects (59, 60). Researchers should also be mindful of the fact that the animal's handler during an AAI session will also vary in their experience and knowledge regarding animal welfare as an additional source of variation (61).

As one of the most commonly studied companion animals in HAI research, dogs in particular exhibit a wide range of characteristics that contribute to variability. With a variety of breeds and sizes of dogs incorporated into companion, therapy, and assistance roles, individual differences in dogs' morphology and disposition are important aspects of variation in HAI literature. For example, physical traits such as a dog's size, coat, eye color, and ear shape have been shown to impact the way that humans perceive dogs (62, 63). In addition, different breeds of dogs can significantly differ in their temperament and behavior (64, 65). For example, some breeds may be more likely to make spontaneous eye contact (66), follow human communicative gestures (67) and be more sociable or playful with humans (68) than others. Even dogs of the same breed category can differ in personality characteristics including playfulness, curiosity, and sociability (69). These individual differences may impact the way that a dog, whether in a pet, therapy, or assistance role, interacts with and potentially bond with humans in the short-term or long-term (70). In the case of pet dogs, studies have found that owners of large dogs spend more time walking their dogs (71) and engage in more training and play with their dogs (72) while small breeds are reported to have more behavioral problems (73). In fact, considering breed-specific variation in analyses is an essential step toward understanding how genetic, physical, and behavioral differences in dogs may explain or predict human therapeutic outcomes. For example, a recent study tracking over 180,000 heart attack victims and 150,000 stroke victims found that dog owners had a lower risk of mortality than non-dog owners (74). However, results varied when considering the breed and size of dogs. Owning a pure-bred retriever breed, for example, was associated with a 40% decrease in mortality rates among the heart attack victims, while owning a companion/toy breed or mixed breed dog had no association with a reduction in mortality (75).

Emerging research has also quantified how differences in dogs' physiological profiles can influence the underlying therapeutic mechanisms of action during HAI. For example, a recent study showed that a population of service dogs selectively bred for friendly and non-aggressive temperaments had higher circulating levels of oxytocin, a neuropeptide involved in human-canine

social interaction and bonding, compared to pet dogs who were not selectively bred (76). Other studies have found that dogs' variation in their oxytocin receptor gene is related to certain breeds of dogs' social behavior when greeting unfamiliar people (77, 78) as well as dogs' attachment behaviors directed to their owners (50). As the oxytocin pathway has been discussed as a potential mechanism underlying positive human-dog interactions (79, 80), these individual differences across dogs may be important for understanding variability across studies.

VARIABILITY IN HUMAN-ANIMAL INTERACTIONS

Thus far, we have discussed variability in both human and animal participants that may contribute to observed variability across HAI research findings. However, one of the most truly variable aspects of this research lies in the nature of the human-animal interactions themselves (i.e., the physical, emotional, and/or psychological interactions that a human and an animal share). In research quantifying the benefits of pet ownership, a specific challenge lies in defining "ownership" and accounting for the variability surrounding this term (81). For example, the human-animal relationship and its resulting effects may differ between those who provide a caregiving role to the animal and those who simply cohabitate with the animal. Dogs, in particular, may also fill several different roles across households including serving as a companion, a surrogate child, or strictly for tasks such as hunting or guarding (82). It is similarly important to consider the varying length of cohabitation time and how much time a human-pet dyad spends together on a daily basis– both of which may have a significant impact on outcomes (83). Not only does the quantity of time have implications for research, but so does the quality of the interactions between an individual and a pet. For example, there is complex variation in daily dog-owner interactions that may contribute to the strength of the human-animal bond ranging from co-sleeping to frequency of cooperative activities such as play or training [e.g., (84, 85)]. Dogs have also been found to form unique attachment relationships to their owners [e.g., avoidant or anxious; (86)] that may be impacted by their owner's caregiving and/or own attachment styles [e.g., (87)]. These sources of heterogeneity have prompted researchers to use a dyadic approach to consider both the attributes of pets and owners to holistically evaluate human-animal relationships (88).

In research assessing outcomes from AAI, interactions can vary widely in terms of activities (e.g., structured or unstructured), setting (e.g., hospital bed, classroom, outdoors), human to animal ratio (e.g., group or individual interaction), and human-animal contact (e.g., duration of petting, talking, or walking). Because of this considerable variation, there is a critical need for manualized protocols and/or detailed reporting of procedures and interactions across studies (89). This will allow for a greater understanding of the benefits from AAI are due specifically to the animal's presence or to other aspects of the intervention such as novelty, attention, or human interaction (12).

During AAI, not only do the components of the interaction contribute to variability, but so does the "dosage" of the intervention in terms of total time spent interacting with an animal. For example, in a systematic review of the effects of AAI for individuals with dementia, the duration of contact with the therapy animal spanned from three, 10-min interactions in one study to bimonthly interactions over 2 years in another (26). In addition, details regarding intervention length, frequency, and content are sometimes not reported. A systematic review of AAI for trauma found that while most articles reported some aspects of the procedures surrounding the participant-animal interaction, not a single article provided enough detail to allow for replication (90). When comparing findings across studies, the omission of these critical details makes it impossible to determine the potential sources of methodological variation. Therefore, it is important for researchers to provide sufficient detail surrounding the characteristics of human-animal interaction, especially in AAI studies, to address this source of variability.

A DISCUSSION OF THE VARIABILITY EXPLAINED BY THE UNIQUE NATURE OF HAI

There is inherent variability linked to the unique nature of HAI, in that, in its simplest form, it involves two complex organisms, a human and a companion animal, interacting in dynamic ways. Not only does HAI research need to account for human psychological, sociological, physiological, and economic variability across humans, but these same variable characteristics apply to the animal as well. For example, a person with financial resources, time, and or motivation to do so, may provide excellent veterinary care, high-quality nutrition, and opportunities for life enrichment to their companion animal that another person with fewer financial resources, less available time, or less motivation may provide to the same species of companion animal. It is important to note that this example is not intended to imply that wealthy people are better caretakers of their companion animals, but rather that each of these variables (financial resources, time, and motivation) are likely to play a role in the care and life enrichment of companion animals that will contribute to variability in pet ownership research. Further, developmental changes must also be taken into consideration. Not only will children interact differently with companion animals than adults and older adults, but each developmental stage may bring a host of unique needs or desires to human relationships with companion animals. On the other side, we cannot neglect the developmental changes taking place in the companion animals as well. Not only will animals also experience physiological, psychological, and behavioral changes as they develop, but also may gain a better understanding of their human counterparts or develop fears or aversions to humans. Therefore, not only do researchers need to keep in mind the inherent variability of the unique nature of HAI, but also how it evolves in both humans and animals over time.

As a field, HAI is charged with understanding not one, but two complex creatures, each with their own needs, motivations,

and capabilities. On the human side, individuals will vary in their experiences, attitudes, abilities, and personalities that shape the way that they perceive, interact with, and ultimately bond with an animal. The animal side of the equation is further complicated by multiple species, each with different species-specific behaviors, welfare needs, physical and mental capabilities, housing and enrichment requirements, and zoonotic disease concerns. Even within the same species, there is immense additional variability in the individual (e.g., breed, temperament, personality, and behavior) that will influence its relationship and interactions with humans. Therefore, research in this field must be mindful of all of these complexities, each of which contribute to the multifaceted nature of human-animal interaction.

While the inherent variability in HAI research contributes to a unique complexity that makes for an interesting field of study, it also makes the field particularly challenging. In particular, a broad spectrum of theoretical considerations is required to account for the variability in the human, the animal, the types of interactions possible, the dynamics of the actual interaction, and any potential constraints imposed by the setting of the interaction (e.g., educational, healthcare). To achieve this, an equally broad spectrum of research methodologies must be incorporated to capture the subtle nuances of the interactions (e.g., qualitative methods) and to tightly control as many aspects of the interactions as possible (e.g., experimental methods).

CONCLUSION AND FUTURE DIRECTIONS

In conclusion, we have described how variability in methods and measurement, human participants, animal participants, and interactions may contribute to mixed findings in the field of human-animal interaction. We have also made suggestions on how to address this variability by using appropriate experimental designs and/or statistical analyses to account for confounding variables, by ensuring detailed reporting of both human and animal characteristics, and by providing thorough descriptions of the duration, context, and structure of human-animal interactions including replicable and/or manualized AAI procedures when possible. However, we have also discussed the inherent complexity of HAI in that even the simplest research study involves considering the dynamic interaction of two complex beings, an animal and a human.

To address the complexity of the field of HAI, researchers must face a variety of theoretical and methodological considerations to account for multiple sources of variability and individual characteristics on both the animal and human level. However, the basic tenets of science apply regardless of the complexity of the topic under study. The field of HAI demands a wide variety of methodologies and measurement, each of which provides important and useful information on which to build the field. However, whatever the approach, the experimental design must be appropriate for the research question and conclusions drawn must be mindful of limitations, including unaccounted for variability that may impact or contextualize findings. It is also incumbent upon researchers to report all results, even nonsignificant findings, as understanding the individuals, contexts, and conditions in which HAI is not beneficial is equally important for the progression of the field.

Although the field of HAI has been characterized by mixed findings, there is a wealth of promising information available on which to expand. With the growth of research in this field, new frameworks continue to emerge to study the relationships between humans and companion animals such as the dyadic approach (88), trans-species methodology (91) and the biopsychosocial model (Gee et al., under review). Inspiration from other fields, such as social psychology (92) developmental psychology (93, 94) and social neuroscience (95), will also continue to inform the theoretical underpinnings of human-animal interactions. The field will continue to benefit from an accumulation of rigorous science while building viable and testable theories. With increased funding opportunities from both public and private sources, knowledge regarding the potential therapeutic outcomes from animal interaction will continue to strengthen by incorporating randomized clinical trial designs and large-scale population studies (96). Although it is a young field, HAI has a promising foundation on which to build, and a firm commitment to scientific rigor will secure its future.

AUTHOR CONTRIBUTIONS

KR, HH, and NG equally contributed to the formation of the manuscript's conceptual ideas and framework. All authors contributed to writing and editing the manuscript.

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Dogs Supporting Human Health and Well-Being: A Biopsychosocial Approach

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Humans have long realized that dogs can be helpful, in a number of ways, to achieving important goals. This is evident from our earliest interactions involving the shared goal of avoiding predators and acquiring food, to our more recent inclusion of dogs in a variety of contexts including therapeutic and educational settings. This paper utilizes a longstanding theoretical framework- the biopsychosocial model- to contextualize the existing research on a broad spectrum of settings and populations in which dogs have been included as an adjunct or complementary therapy to improve some aspect of human health and well-being. A wide variety of evidence is considered within key topical areas including cognition, learning disorders, neurotypical and neurodiverse populations, mental and physical health, and disabilities. A dynamic version of the biopsychosocial model is used to organize and discuss the findings, to consider how possible mechanisms of action may impact overall human health and well-being, and to frame and guide future research questions and investigations.

Keywords: dog, human health, human-animal interaction, biopsychosocial, canine, mental health

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INTRODUCTION – A HISTORICAL PERSPECTIVE ON DOG-HUMAN RELATIONSHIPS

The modern relationship between humans and dogs is undoubtedly unique. With a shared evolutionary history spanning tens of thousands of years (1), dogs have filled a unique niche in our lives as man's best friend. Through the processes of domestication and natural selection, dogs have become adept at socializing with humans. For example, research suggests dogs are sensitive to our emotional states (2) as well as our social gestures (3), and they also can communicate with us using complex cues such as gaze alternation (4). In addition, dogs can form complex attachment relationships with humans that mirror that of infant-caregiver relationships (5).

In today's society, dog companionship is widely prevalent worldwide. In the United States, 63 million households have a pet dog, a majority of which consider their dog a member of their family (6). In addition to living in our homes, dogs have also become increasingly widespread in applications to assist individuals with disabilities as assistance dogs. During and following World War I, formal training of dogs as assistance animals began particularly for individuals with visual impairments in Germany and the United States (7). Following World War II, formal training for other roles, such as mobility and hearing assistance, started to increase in prevalence. Over the decades, the roles of assistance dogs have expanded to assist numerous disabilities and

conditions including medical conditions such as epilepsy and diabetes and mental health disorders such as posttraumatic stress disorder (PTSD). At the same time, society has also seen increasing applications of dogs incorporated into working roles including detection, hunting, herding, and protection (8, 9).

In addition to these working roles, dogs have also been instrumental in supporting humans in other therapeutic ways. In the early 1960s, animal-assisted interventions (AAI) began to evolve with the pioneering work of Boris Levinson, Elizabeth O'Leary Corson, and Samuel Corson. Levinson, a child psychologist practicing since the 1950s, noticed a child who was nonverbal and withdrawn during therapy began interacting with his dog, Jingles, in an unplanned interaction. This experience caused Levinson to begin his pioneering work in creating the foundations for AAI as an adjunct to treatment (10). In the 1970s, Samuel Corson and Elizabeth O'Leary Corson were some of the first researchers to empirically study canine-assisted interventions. Like Levinson, they inadvertently discovered that some of their patients with psychiatric disorders were interested in the dogs and that their patients with psychiatric disorders communicated more easily with each other and the staff when in the company of the dogs (11, 12). Over the following decades, therapy dogs have been increasingly found to provide support for individuals with diverse needs in a wide array of settings (13).

THEORETICAL FRAMEWORK FOR DOG INTERACTION BENEFITS

For over 40 years, the biopsychosocial model (14) has been widely used to conceptualize how biological, psychological, and social influences combine to determine human health and well-being. Biological influences refer to physiological changes such as blood pressure, cortisol, and heart rate, among others; psychological influences include personality, mood, and emotions, among others; and social influences refer to cultural, socio-economic, social relationships with others, family dynamics, and related matters. **Figure 1** presents a graphical illustration of the relationship among these three influences in determining overall health and well-being. Although the model has dominated research and theory in health psychology for decades, more recently, it was re-envisioned as a more dynamic system (15) that construes human health as the result of the reciprocal influences of biological, psychological and social factors that unfold over personal and historical time. For example, if a person breaks his/her arm, there will be a biological impact in that immune and muscle systems respond and compensate. Social, or interpersonal, changes may occur when support or assistance is offered by others. Psychological changes will occur as a result of adjusting to and coping with the injury. Thus, the injury represents a dynamic influence initiated at one point in time and extending forward in time with diminishing impact as healing occurs.

This dynamic biopsychosocial approach to understanding health and well-being is appealing to the field of human-animal interaction (HAI) because of the dynamic nature of the relationship between humans and animals. For example, a person may acquire many dogs over his/her lifetime, perhaps from childhood to old age, and each of those dogs may sequentially develop from puppyhood to old age in that time. Behaviorally, the way the human and the dog interact is likely to be different across the lifespans of both species. From a biopsychosocial model perspective, the dynamic nature of the human-canine relationship may differentially interact with each of the three influencers (biological, psychological, and social) of human health and well-being over the trajectories of both beings. Notably, these influencers are not fixed, but rather have an interactional effect with each other over time.

While a person's biological, psychological, and social health may affect the relationship between that person and dogs with whom interactions occur, the focus of this manuscript is on the reverse: how owning or interacting with a dog may impact each of the psychological, biological, and social influencers of human health. We will also present relevant research and discuss potential mechanisms by which dogs may, or may not, contribute to human health and well-being according to the biopsychosocial model. Finally, we will emphasize how the biopsychosocial theory can be easily utilized to provide firmer theoretical foundations for future HAI research and applications to therapeutic practice and daily life.

Psychological Influences

Much research has been conducted on the impact of dog ownership and dog interactions on human psychological health and functioning. Frequent interactions with a dog, either through ownership or through long-term interventions, have been associated with positive psychological outcomes across the lifespan [for a systematic review of this evidence see (16)]. One psychological aspect of interest to many HAI researchers is depression, especially among older adults. However, the relationship of pet dog ownership and depression over the lifespan continues to have inconsistent and inconclusive findings (16). Nevertheless, there are examples in the literature highlighting the beneficial role of dog ownership in reducing depression. As is frequently the case in HAI, the evidence from intervention studies is stronger than that of pet ownership studies (16), with the preponderance of this evidence linking animal-assisted interventions to a decrease in depression, as measured by self-report indices. Among the mechanisms for this reduction in depression are biological and social influences. For example, one such study found that an attachment relationship with a pet dog may serve as a coping resource for older women by buffering the relationship between loneliness (also measured by self-report indices) and depression, such that the presence of the pet dog appears to ameliorate the potential for loneliness to exacerbate depression (17). A causal relationship between dog ownership and mental health is difficult to determine. Not only may owning a pet dog increase stress, but those who are already suffering from loneliness or depression may be more inclined to have a pet dog than those who do not.

Another psychological outcome related to dog interaction that receives considerable research attention is anxiety. Studies have found that short-term, unstructured interactions with a therapy dog can significantly reduce self-reported anxiety and

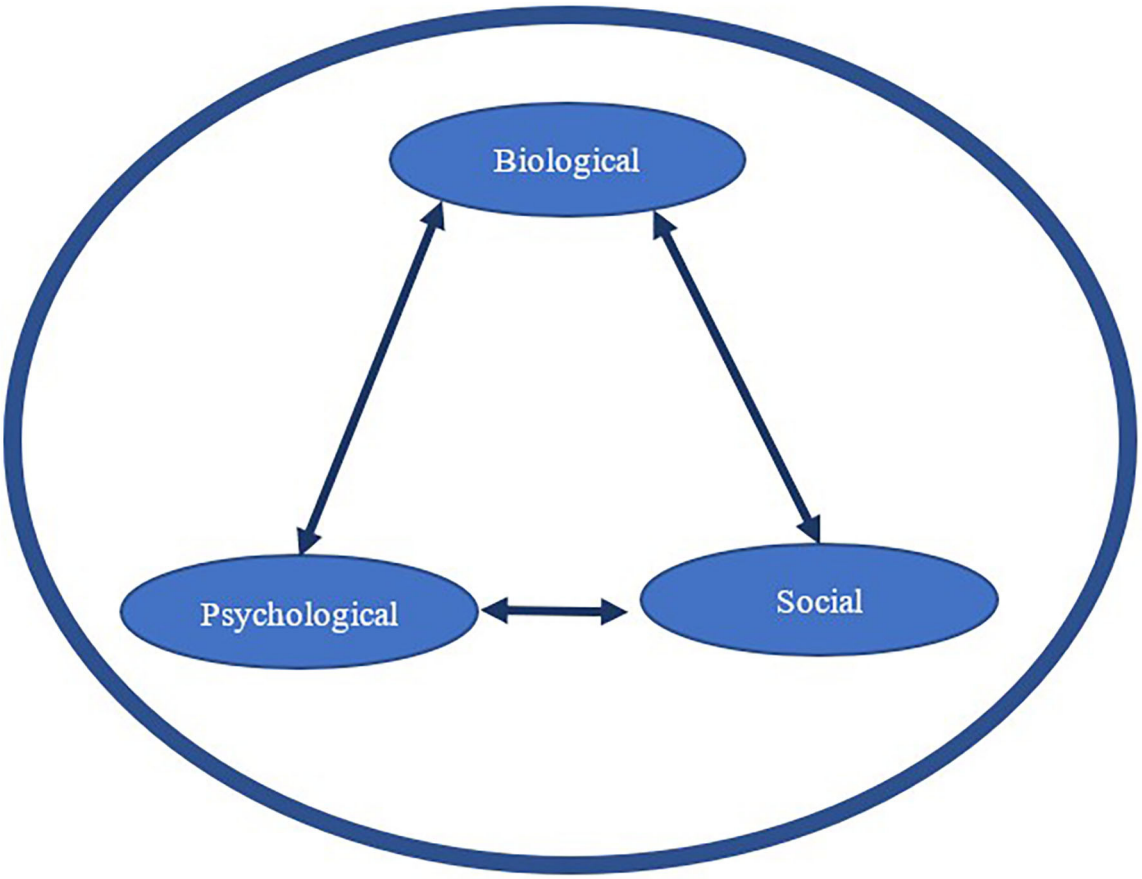

FIGURE 1 | A biopsychosocial perspective of how biological, psychological, and social influences may impact one another (solid lined arrows) and influence human health and well-being (represented here by the large thick circular shape).

distress levels [e.g., (18)]. For example, children with their pet dog or a therapy dog present during a stressful task exhibit lower perceived stress and more positive affect compared to when alone (19), when a parent was present (20), or when a stuffed dog was present (21). In addition to psychological mechanisms, there are social and biological mechanisms at play as well. In these short-term stressful contexts, a dog may serve as both a comforting, nonjudgmental presence as well as a positive tactile and sensory distraction. Dog interaction might also reduce anxiety and distress by influencing emotion regulation while coping with a stressor (22). During animal-assisted therapy, having a dog present during psychotherapy such as cognitive behavioral therapy can aid in decreasing self-reported anxious arousal and distress for patients who have experienced trauma, making the therapeutic treatment process more effective (23).

In addition to the negative aspects of psychological functioning, HAI research has also aimed to quantify the effects of dog interaction and ownership on positive psychological experiences such as happiness and well-being. Some studies have found that dog ownership is associated with higher life satisfaction and greater well-being (24), while other studies show that this is the case only when the dog provided social support (25) or satisfied the owner's needs (26). However, other large-scale surveys have found no significant differences in self-reported happiness between dog owners, cat owners, and non-pet owners (27), contributing to mixed findings. Recent discussions argue that too much focus has been placed on the relationship between mental health and the simple variable of dog ownership, when the specific activities that owners engage in with their dogs (e.g., walking, tactile interaction, and shared activities,) may be more important in explaining positive well-being (28). Further, many other factors may be driving these inconsistent findings in depression, anxiety, and well-being, including the owner's personality (24), gender and marital status (29), and attachment to the dog (30).

Dogs may also provide a source of motivation; for example, people with dogs are more likely to comply with the rigors of their daily life (31). The relationship with a pet dog may provide motivation to do things that may be less desirable. For example, for older adults who own pets, it is not uncommon for them to be more involved in daily life activities because of the need to take care of their animals (32). Likewise, children also complete less desired activities due to their relationship with the dog [for a discussion of this topic see (33)].

An accumulation of research also suggests that dog interaction may have specific psychological benefits for individuals with physical disabilities and chronic conditions. Cohabitating with a specially trained assistance dog, including guide, hearing, and service dogs, can be associated with increased psychological and emotional functioning among individuals with disabilities (34). For individuals with mental disorders such as posttraumatic stress disorder (PTSD), recent research has also found that having a psychiatric service dog is associated with fewer PTSD symptoms, less depression and anxiety, and better quality of life [For a review see (35)]. These benefits appear to be due to a combination of the service dog's specific trained tasks and aspects inherent to cohabitating with a pet dog, including having a source of love, nonjudgmental social support, and companionship (36).

Similar research has also highlighted the value of dogs for children with disorders of executive functioning and self-regulation, especially autism spectrum disorder (ASD) and attention-deficit/hyperactivity disorder (ADHD). For some children with ASD, dogs may provide a calming and positive presence (37) and may both reduce anxiety (38) and improve problematic behaviors (39). Parents report that both pet dogs and service dogs can provide certain benefits for children with ASD, including benefits to children's moods, sleep, and behavior (40, 41). Therapy dogs have also been found to be impactful in supporting children with ADHD in their emotional regulation (42) and aspects of character development (43). Nevertheless, the outcome of dog interactions may not be positive for all individuals with ASD and ADHD; despite evidence of psychological benefits of dog interaction for some children, others may be fearful or become over-stimulated by dogs (44).

In addition to impacts on psychological health, dog interaction can also impact psychological functioning, cognition, and learning. Among children, emerging research suggests short-term interactions with a therapy dog may lead to improvements in specific aspects of learning and cognition. A recent systematic review of research on therapy dog reading programs indicated that reading to a dog has a number of beneficial effects including improved reading performance (45). Studies suggest that interacting with a therapy dog may also improve speed and accuracy on cognitive (e.g., memory, categorization, adherence to instructions) and motor skills tasks among preschool-aged children compared to interacting with a stuffed dog or human (46). Similarly, a recent study showed that 10–14-year-old children had greater frontal lobe activity in the presence of a real dog as compared to a robotic dog, indicating a higher level of neuropsychological attention (47).

Among young adults, similar effects on cognition and learning have been found. Numerous colleges and universities now offer interactions with therapy dogs, typically during high stress times (such as before exams). In this sense, a biological mechanism through which dog interaction may positively impact cognition and learning is via stress reduction and improvement in positive affect. Even such short and infrequent interactions with therapy dogs may decrease perceived stress and increase perceived happiness in college students [e.g., (48, 49)]. Further, some institutions have permanent resident therapy dogs and/or long-term intervention programs; one such program showed that students who interacted with therapy dogs for 8 weeks reported significantly less homesickness and greater satisfaction with life than wait-listed controls (50). These effects may translate to additional effects on students' academic success, learning, and cognition. For instance, a recent randomized controlled trial (51) paired a standard academic stress management program with therapy dog interaction; the pairing produced significantly higher levels of self-reported enjoyment, usefulness, self-regulation, and behavior change than the stress management program or dog interaction alone. However, when therapy dog interaction is closely paired with more specific learning experiences, beneficial effects on stress remain, but benefits to academic performance may not manifest. For example, a recent study showed that interacting with a therapy dog resulted in significant improvements in students' perceived stress and mood, but not in actual exam scores (52). Similarly, interacting with a therapy dog during the learning and recall phase of a memory test did not improve memory compared to a control group (53). Taken together, dog interaction may improve stress and affect among college-aged adults as well as dimensions important for academic success and learning, but these results may or may not translate to cognitive performance benefits.

Biological Influences

The psychological and biological effects of HAI are often closely interwoven, as seen in the Psychological Influences section above and as demonstrated by the frequency with which psychological effects are evaluated using biological assessments of stress, anxiety, and arousal (54). For example, a plethora of studies have examined how short-term interactions with dogs can influence stress by measuring physiological biomarkers. Studies have found that dog interaction can influence parameters such as blood pressure, heart rate, and electrodermal activity (55) as well as neurochemical indicators of affiliative behavior [e.g., beta-endorphins, prolactin, and dopamine; (56)].

However, one of the most popular physiological measures in HAI research is the stress hormone cortisol (57). Studies have found that short-term interactions with a dog can decrease both subjective stress and circulating cortisol concentrations [e.g., (58)]. Cohabitating with a dog has also been found to impact circulating cortisol after waking among children with ASD (39) and military veterans with PTSD (59). Experimental studies have also examined how having a dog present may modulate the stress response and cortisol secretion among individuals undergoing a stressful situation. Among adults, studies have found that having a dog present during a socially stressful paradigm can attenuate cortisol compared to when alone or with a human friend (60). A recent randomized controlled trial similarly found that interacting with a therapy dog, for 20 min, two times per week, over a 4-week period resulted in reduced cortisol (basal and diurnal measurement) among typically developing and special needs school children compared to the same duration and length of delivery for a yoga relaxation or a classroom as usual control group (61). However, it is of note that many methodologically rigorous studies have not found significant effects of interacting with a dog on physiological parameters, including salivary cortisol (21, 62, 63). A recent review of salivary bioscience

research in human-animal interaction concluded that significant variation exists with regards to sampling paradigms, storage and assaying methods, and analytic strategies, contributing to variation in findings across the field (57).

As research quantifying the physiological outcomes from dog interaction continues to increase, so does research attempting to understand the underlying mechanisms of action leading to stress reduction. One theoretical rationale for dogs' stress-reducing benefits consists of the dog's ability to provide non-judgmental social support (60), improve positive affect (64), and provide a calming presence (22). Dogs may also contribute to a feeling of perceived safety and provide a tactile and grounding comfort (65). For these reasons, dogs are often incorporated into treatment and recovery for individuals who have experienced a traumatic event (66). Another mechanism contributing to these stress reducing benefits may be tactile stimulation and distraction derived from petting or stroking a dog. For example, Beetz et al. (67) found that the more time a child spent stroking the dog before a stressful task, the larger the magnitude of cortisol decrease. In fact, calming tactile interactions such as stroking, touching, and petting may be a key mechanism explaining animal-specific benefits to stress physiology, as touch is more socially appropriate in interactions with animals than as with other people (22). While there are many hypothesized mechanisms underlying positive psychophysiological change following human-dog interaction, more research is needed to determine how individual differences in humans, animals, and the human-animal relationship affects outcomes (21, 57, 62, 63).

Another mechanism in which positive dog interaction may result in psychophysiological benefits is via the secretion of oxytocin. Oxytocin not only buffers the stress response and cortisol secretion (68) but is also involved emotion, trust, and bonding (69). The oxytocin system has been hypothesized to be a primary mechanistic pathway involved in human-dog interactions (70). Positive dog-owner interactions including stroking, petting, and talking have been shown to result in increased oxytocin levels in both dog owners and dogs, which has been related to the strength of the owner-dog relationship (71) and dog-human affiliative behaviors (72, 73). Some studies have also found differential effects in oxytocin reactivity after dog interaction between human males and females (74), giving context to potential gender and/or hormonal differences in dog-human interactions. However, even though the oxytocin system exhibits potential as a pathway by which dogs provide psychophysiological benefits, it should be noted that mixed findings and methodological and measurement differences limit strong conclusions (75).

In regards to pet dog ownership, many studies have also sought to understand the biological effects of long-term interactions with a pet dog. Some research suggests that sharing animal-associated microbes with a pet dog can have long-term impacts on human health (76) while others have found that cohabitating with a pet dog can be beneficial for child allergies (77) and immune system development (78). However, most research on the long-term health impacts of pet dog ownership has focused on cardiovascular functioning. Epidemiological research suggests that dog ownership is linked to greater physical activity levels (presumably linked to dog-walking), and reduced risk for cardiovascular disease, stroke, and all-cause mortality [for a summary see (79)]. A recent meta-analysis of ten studies amassing data from over three million participants found that pet dog ownership was associated with a 31% risk reduction for mortality due to cardiovascular disease (80). However, dog ownership research of this nature will always suffer from an important chicken and egg type question: do dogs make us healthier, or do healthy people opt to own dogs?

Social Influences

A final way in which dog companionship and interaction may contribute to human health and well-being is through the social realm. Dogs may impact social functioning by providing direct social support (81) and a source of an attachment bond (82) which in turn may contribute to better social and mental health by providing companionship. Acquiring a pet dog has been reported to reduce both short-term and long-term self-reported loneliness (83). Particularly for those who live alone, dog ownership may serve as a protective factor against loneliness in times of social isolation, such as during the COVID-19 pandemic (84). Among older adults living in long-term care facilities or who live alone, dog visitation may also decrease loneliness by providing a source of meaningful companionship and social connectedness (85, 86). However, the literature on pet dogs and loneliness is also characterized by mixed findings, raising the possibility that dog ownership may be a *response* to loneliness rather than *protection* from loneliness. Further, there remains a lack of high quality research in this area which limits any causal conclusions (87).

Another way in which the social support from a pet dog may benefit social functioning is by facilitating social interactions with others. For example, observational studies have found that being accompanied by a dog in public increases the frequency of received social interactions (88) and social acknowledgments [e.g., friendly glances, smiles; (89)]. For those who engage in dog walking, social interactions are perceived as a rewarding side effect (90). Dogs can also provide a source of social capital, defined as the glue that holds society together (91). The research of Wood and colleagues (92) suggests that dogs can function as facilitators for social contact and interaction, with pet owners reporting higher perceptions of suburb friendliness and more social interactions with neighbors compared to non-pet owners.

For children and adolescents, pet dog ownership may contribute to healthy social development. Positive child–pet dog interactions have been shown to have benefits to children's social competence, interactions, and play behavior [for a review see (93)]. Not only can children form attachment relationships with dogs (94), but pet dogs may promote feelings of safety and security (95) that can facilitate childhood social development. Pet ownership may also help children develop skills to form and maintain social relationships with their peers (96). For example, cross-sectional studies found that children with a pet dog in the home have fewer peer problems and have more prosocial behavior with children without a dog [e.g., (97, 98)].

Among children with developmental disorders, dog interaction has also been similarly shown to impact social

functioning. For children with ADHD, two randomized controlled trials have found that 12 weeks of visits with a therapy dog, incorporated into curricula designed to improve skills and reduce behavioral problems, can result in improved social skills, prosocial behaviors, and perceptions of social competence (42, 43). One potential explanation for these benefits is that children may interpret the dogs' nonverbal communication as less threatening and easier to interpret than human interaction (99, 100). A recent eye-tracking study found that children with ASD exhibit a bias in social attention to animal faces, including dogs, compared to human faces (101). The presence of a dog in clinical applications may also promote more social engagement with a therapist while reducing negative behaviors (102, 103). Further, there is some evidence that having a pet dog in the home can have a positive impact on social interactions of children with ASD, especially among verbal children, while teaching children responsibility and empathetic behavior (104, 105).

POTENTIAL MECHANISMS OF ACTION

We have discussed how, in the psychological realm, interacting with a dog can positively relate to depression, anxiety, and well-being as well as psychological functioning in the areas of cognition, learning, and attention. It is interesting to note that most psychological constructs are measured using self-report indices, such as the Beck Depression Inventory (106) or the UCLA Loneliness Scale (107), while a smaller group of constructs are measured using speed and accuracy to detect targets (attention) or to remember information (learning and memory). In the biological realm, we discussed how interacting with dogs can influence stress-related physiological parameters and long-term biological and cardiovascular health. Biological measures are often recorded in real-time, such as heart rate or blood pressure, or are collected at critical time points during the study (e.g., saliva, urine, or blood samples for such measures as cortisol or oxytocin). Finally, we discussed the social realm, in which interacting with a dog can provide social support, facilitate social interactions, and improve social development and social skills. Measures used to assess variables in the social realm include self-report indices (e.g., demographics such as marital status, numbers of family members and friends), real time observations of social interactions (e.g., video analyses of interactions using ethograms), and parent/teacher reports of social functioning [e.g., Social Skills Rating System; (108)]. To better understand and organize these various findings, we now consider potential mechanisms of action in the context of the biopsychosocial model, and as part of this discussion we will consider the potential for different types of measurement to have their own influence.

The mechanisms that underly positive human-dog interactions are likely to be interrelated and broadly, yet differentially, impactful across the three influencers of health (biological, psychological and social). According to the biopsychosocial model, impacts on one of the influencers of health is likely to impact the others (14). Further, an underlying mechanism of change may have a larger immediate impact on one realm than on the other two (15). Although this applies to the many influences we have discussed above, we will describe a reduction in stress as a more detailed example of how the biopsychosocial model can be considered. Stress is likely to have an immediate and measurable impact on the biological system through endocrinological (e.g., changes in cortisol) and psychophysiological (e.g., changes in blood pressure) processes. This same reduction in stress is likely to impact the psychological system through changes in mood or affect, concentration, and motivation, but that impact may not be immediately measurable or may be smaller in magnitude. This conjectured delay or reduction in effect size stems at least in part, from the way these changes are typically measured and the time course for potential effects to become measurable. For example, some biological changes indicative of increased stress (e.g., heart rate) can be measured in direct correspondence with the experimental manipulations (e.g., interacting with the dog vs. experiencing a control condition), and provide real time biological indications of changes in stress levels. Psychological indications of stress may be measured by a self-report survey instrument assessing state or trait anxiety. This type of measure cannot be completed in real time during the various experimental conditions (e.g., interacting with the dog vs. experiencing a control condition), but must be completed at some point following the experimental manipulation. It is possible that psychological measures are not as immediately sensitive to changes in the constructs they measure because of the required delay between manipulation and measurement. Such a delay may underestimate the real time effect as it may fade over time. Finally, reductions in stress have the potential to impact social systems by increasing social approaches and acceptance of approaches by others, but that impact may be of a small size or require even more time to be measurable. For example, exposure to stress may have immediate physiological effects, but it could take more time (prolonged exposure to stress) for those effects to impact some measures of social influence such as number of friends.

In **Figure 2**, the mechanism of stress reduction is used as one example for the purposes of this discussion to exemplify how human-dog interactions may influence human health and well-being, as explained by the biopsychosocial model. Stress reduction may have a more immediate or larger impact on the biological realm as demonstrated by the larger arrow, while having a smaller (or perhaps delayed) impact on the psychological realm and an even smaller (or potentially more delayed) impact on the social realm.

Based on the research described earlier, we have seen that interacting with a dog can have stress reducing impacts in the biological realm such as decreased cortisol, heart rate, and blood pressure, and increases in oxytocin. In the psychological realm, stress reduction can be a driver of immediate improvements in self-report measures of stress, mood, and anxiety and more delayed improvements in overall mental health and quality of life. The social realm is also likely to be directly and indirectly impacted by this stress reduction from both immediate and delayed psychophysiological changes as well as more long-term improvements in social support, social networks, social development, and overall social health. Therefore, it is

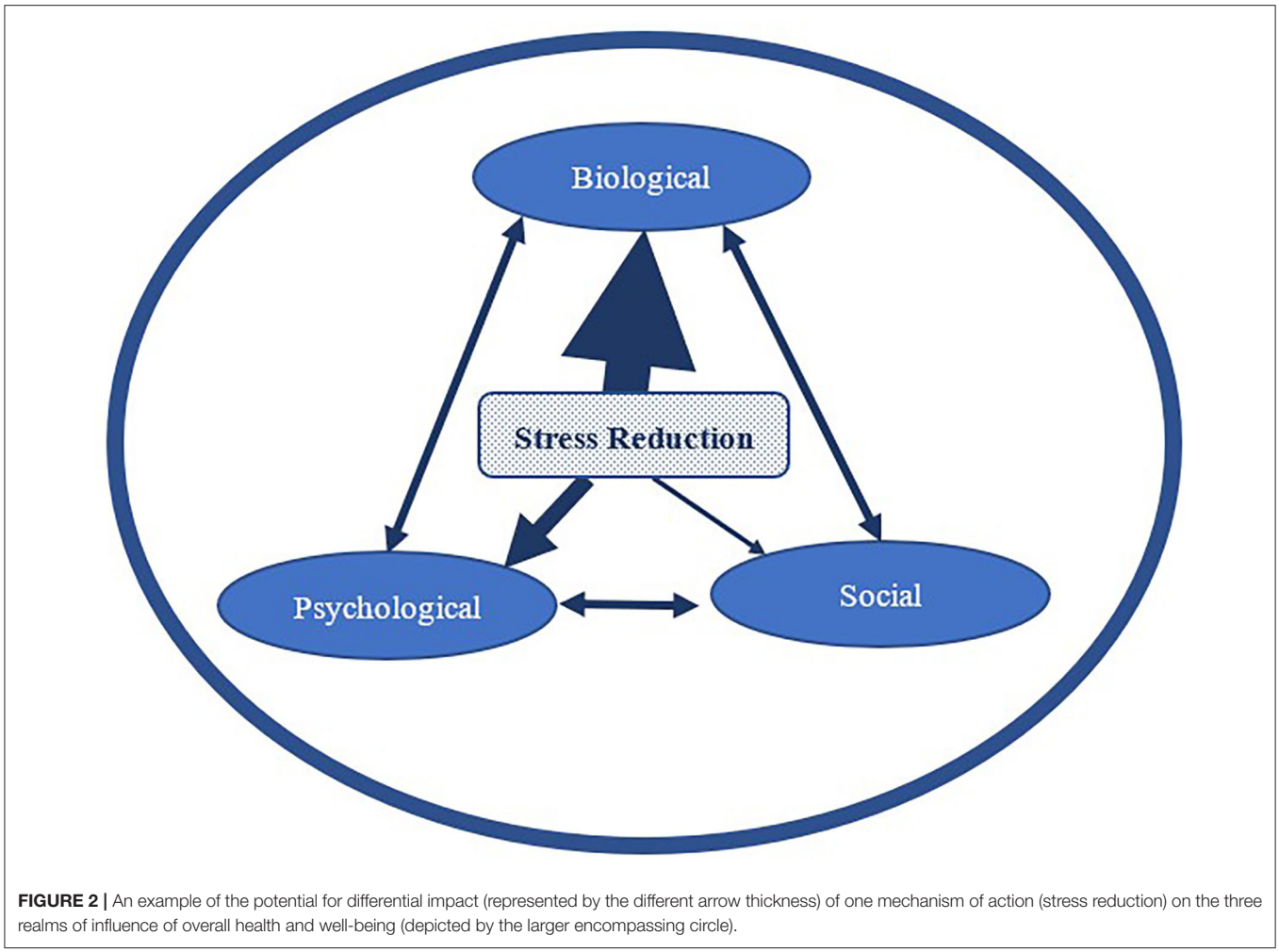

FIGURE 2 | An example of the potential for differential impact (represented by the different arrow thickness) of one mechanism of action (stress reduction) on the three realms of influence of overall health and well-being (depicted by the larger encompassing circle).

important to consider the dynamic nature of these three realms in that there may be a strong immediate effect of dog interaction on one realm, but a lesser, delayed impact in the other two realms. Similar to our more detailed example of stress above, other influences we have discussed (e.g., social support, positive affect, etc.) are likewise mechanisms that operate in a similar reciprocal biopsychosocial framework. Further, although it likely that the three influences are interrelated, it is not known from the current evidence the degree to which they may be interrelated and thus have shared and overlapping effects on one another and on overall health and well-being. Therefore, a consideration of mechanisms that influence human-dog interactions from a dynamic and flexible biopsychosocial perspective, instead of from a single realm, is an important addition to the study of human-animal interaction.

CONCLUSION AND FUTURE DIRECTIONS

In conclusion, the biopsychosocial model is a promising theoretical model to be applied to human-animal interaction research for several reasons. First, the field of HAI has been plagued by mixed findings in which some research suggests that dogs have beneficial effects on human health and well-being and others suggest no effect or even a negative effect [for a discussion see (109)]. This variability in HAI research outcomes caused by differing methodologies, measurement, populations, and interventions is described in detail by Rodriguez et al. (110). However, we also argue that some of the variability seen in HAI research may be explained by the potential for differential immediate and delayed impacts within each of the three biopsychosocial model realms. For example, if dog interaction shows immediate reduction in physiological measures of stress, how long does that reduction last, and do we see corresponding immediate and/or delayed responses in the psychological and social realms? Therefore, more information about differential impacts of dog interactions on each of the three influencers at various points in time is needed. In addition, it may be necessary to apply a variety of measures (at least one measure per influencer realm) over time to fully disentangle the existing mixed results in the field of HAI.

Secondly, due to the flexibility that this dynamic biopsychosocial model offers in explaining HAI research outcomes, we propose this model as an effective avenue to promote future theoretically grounded research in our field.

Saleh (111) stresses that practice, research, and theory are the corner stones of any field, HAI is not exempt from this consideration. The field of HAI will benefit from applying an accepted model, like the biopsychosocial model, because it provides a useful framework for understanding and predicting how interactions between humans and animals impacts human health and well-being. As Saleh (111) explains, "it is the result of the relationship between the process of inquiry (research) and the product of knowledge (theory)" that our understanding of a process may become clearer. Therefore, current research should continue to modify and impact a present theory, which should act as a guide for researchers to constantly generate and test the basis of a theory (111). The findings from such theory-driven research could then help practitioners, as well as health care policy makers, in how to effectively incorporate dogs in therapeutic settings and in homes.

Lastly, the reciprocal relationship of the psychological, biological, and social domains can be used to elucidate the mechanisms that both impact and are impacted by interactions between humans and animals. Theory-driven science (for which we have proposed the biopsychosocial model as a useful framework) should be used to influence and inform research, practice, and policy. Thus, researchers and practitioners applying the biopsychosocial model will be instrumental not only in guiding future research in the field, but also in clarifying existing research as well people's perceptions of benefits derived from canine-human interactions.

AUTHOR CONTRIBUTIONS

NG provided the initial organization and theoretical framework. All authors wrote and edited the document in shared collaboration and discussed and conceived the idea for the paper.

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Canine-Assisted Interventions in Hospitals: Best Practices for Maximizing Human and Canine Safety

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Canine-assisted interventions (CAI) are becoming more popular in hospital settings, representing a crucial intersection between animals, veterinary medicine, and society. However, standardized policies and procedures to minimize risk and maximize benefit to vulnerable humans and protect therapy dog welfare are lacking, posing a challenge to safe practice. Few intervention programs are evaluated to document efficacy compounding the potential risk. This paper presents a rationale for CAI in hospitals and describes the evidence, issues, and challenges to establishing and maintaining safe and effective programs for humans and animals. Recommendations are made for best practices based on the existing scientific evidence and a model program in place in a major medical center for 19 years. Scientific and practical implications are considered.

Keywords: animal-assisted intervention, best practices, human–animal interaction, canine-assisted intervention, human–canine interaction

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INTRODUCTION

Hospitalized patients represent a vulnerable population as they face not only the challenges of their medical conditions and treatments, but also separation from familiar settings and social supports. Recognizing the distress associated with hospitalization, administrators, and clinicians seek novel, complementary, and cost-effective interventions to provide comfort and support to patients. Perhaps in part due to broad media claims of patient benefits, canine-assisted interventions (CAI) are becoming more popular in hospital settings. However, both a lack of consistent practice standards and evidence of program efficacy pose risks to patients, hospital employees, therapy dogs, and dog handlers. This paper describes the evidence, issues, and challenges for CAI programs to practice safely and effectively in hospital settings and provides recommendations for best practice based on scientific evidence and a model program.

EVIDENCE OF CANINE-ASSISTED INTERVENTION EFFICACY

Benefits of Human–Animal Interaction

Humans have shared their lives with companion animals for thousands of years, yet it has only been over the past three to four decades that researchers have turned their attention to the possible health benefits of this relationship (1). The health outcomes and populations studied are widely varied and although there are some promising findings, overall, results have been mixed. The areas with the most substantial evidence supporting health

benefits of human–animal interaction are cardiovascular disease risk and stress reactivity. Research on cardiovascular benefits of pet ownership was launched by a 1980 seminal study documenting decreased mortality in pet owners 1 year after discharge from a coronary care unit (2). Further research supported these findings in a sample of pet owners participating in the large Cardiac Arrhythmia Suppression Trial (3). Social support ant pet (particularly dog) ownership predicted 1-year survival for survivors of myocardial infarction, independent of demographics, disease severity, and other psychosocial factors. Decreased cardiovascular disease death was also reported in a longitudinal study of a nationally representative sample of pet owners without major physical illness (4). In this study cat ownership was significantly associated with reduced risk of death, particularly from stokes.

Other studies documenting reduced cardiovascular reactivity in pet owners followed. Married couples owning dogs or cats had lower baseline diastolic and systolic blood pressure than couples without pets and showed lower reactivity and faster recovery to mental and physical stressors (5). Lower cardiovascular reactivity to mental stress was also found in adults with borderline hypertension randomly assigned to obtain a cat or dog and start ACE inhibitor therapy compared with those on angiotensin-converting enzyme inhibitor therapy only (6). Systolic blood pressure, heart rate, and renin activity were significantly lower in the pet owning group. Lower physiological stress has also been reported in military veterans with post-traumatic stress disorder living with service dogs (7).

Lower systolic and diastolic blood pressure were found in older adults with pre- to mild hypertension when their pet dogs were present during their normal daily lives (8). Similarly, a large Australian study of cardiovascular risk factors in pet owners and non-owners attending a free medical screening reported pet owners had lower systolic blood pressure and triglycerides, and exercised more (9). More recently researchers analyzed data from 24-h heart rate monitoring of pet and non-pet owners and determined that pet ownership served as an independent modulator of cardiac autonomic imbalance in patients with diabetes mellitus, hypertension, and hyperlipidemia (10).

After a critical review of studies such as these, an American Heart Association scientific statement was published concluding that "pet ownership, particularly dog ownership, is probably associated with reduced cardiovascular risk" and "pet ownership, particularly dog ownership, may have some causal role in reducing cardiovascular disease risk" [Levine et al. (11), p. 2356].

Benefits of Canine-Assisted Interventions in Hospitals

A natural extension of this body of work is to examine whether humans in settings without dogs, such as hospitals, can benefit from safely interacting with unfamiliar dogs, as is the case when interacting with visiting therapy dogs. An exploratory study compared physiological benefits of dog owners interacting with their own therapy dog vs. an unfamiliar therapy dog in a clinic setting (12). This small study examined patterns of physiological reactivity (salivary cortisol, systolic and diastolic blood pressure, heart rate, brain waves) to a mental stressor and found consistent patterns of increased stress associated with the stressor and consistent patterns of relaxation associated with interacting with a therapy dog in both conditions. Relaxation patterns observed interacting with an unfamiliar therapy dog were consistent with those observed when interacting with one's own dog and self-reported anxiety and stress were similar in both conditions, providing preliminary support for further study of CAI in healthcare settings.

Although studies have emerged supporting the benefits of CAI in hospital settings, little consistency exists in the clinical populations studied, outcomes, and methodologies emphasizing the need for more studies in this area. Inpatient psychiatry is one area with more consistent evidence of patient benefits. An early study of the effect of CAI on anxiety in hospitalized psychiatry patients yielded promising findings. Patients with mood, cognitive, psychotic, or other disorders had lower anxiety scores on the State-Trait Anxiety Inventory after participating in recreational therapy incorporating a CAI (13). Although between group differences were not significant, only patients with mood disorders had lower anxiety scores in the comparison group receiving traditional recreational therapy without a dog present. Similar findings were reported in a crossover study of acutely depressed patients assigned to CAI and a control condition (14). State-Trait Anxiety Inventory scores were lower in the CAI condition.

Other studies reporting CAI benefits for hospitalized psychiatric patients found reductions in fear prior to electroconvulsive therapy in patients randomly assigned to a 15-min CAI vs. magazines (15), greater reductions in depression, anxiety, pain, and pulse in patients receiving CAI compared to a comparison stress management program (16), qualitative references by adolescent patients to a CAI therapy dog as a friend or therapist and increased interactions on the psychiatric unit promoted by a CAI (17), and enriched therapeutic contact and enhanced patient openness and treatment adherence associated with CAI on a psychiatric service (18). Two studies reported increased attendance by psychiatry patients in group therapies involving CAI compared to group therapies without CAI (19, 20). Several studies have focused on benefits of CAI specifically for inpatients with schizophrenia. Improvements in negative symptomatology, greater treatment adherence, and reduction in cortisol levels were reported in patients randomly assigned to psychosocial rehabilitation including CAI (21). Benefits were also found for patients randomly assigned to weekly CAI for 2 months with improvements in self-esteem, self-determination, and positive psychiatric symptoms (22). Hospitalized elderly patients with schizophrenia were the focus of another study, reporting improvements in socialization, well-being, and activities of daily living following 12 months of weekly CAI (23).

Although several studies have investigated the effects of CAI on pediatric patients, results have been mixed with two randomized controlled studies reporting no effect on biobehavioral stress (24), or self-reported anxiety or pain (25). Similar null findings were found in a study of physiological stress, anxiety, and medical fear in pediatric patients assigned

to CAI or a comparison condition (26). In contrast, other studies have reported positive findings, including reductions in anxiety in a convenience sample of pediatric patients assigned to CAI compared to a control group (27), greater reductions in physiological and behavioral distress in children undergoing a physical exam with a dog present compared with those in a control group (28), and less distress and lower cortisol levels in pediatric patients when participating in CAI before, during, and after venipuncture compared with a control group (29). As with dog ownership studies, varying methodologies, techniques for sampling biomarkers, samples and sample sizes, and target outcomes likely contribute to the mixed findings seen in CAI studies. Advances in technology and assessment methods informing later studies likely contribute to differences as well.

Other hospitalized patient populations have been the focus of one or two studies of CAI indicating potentially positive effects, but further study is needed with these populations to confirm results. For example:

- Patients randomly assigned to CAI prior to cystoscopy had lower anxiety and stress levels than a treatment as usual control group (30)
- Patients randomly assigned to physical therapy incorporating CAI following total joint arthroplasty reported less pain and higher satisfaction with their hospitalization than those assigned to standard physical therapy (31).
- Following total joint replacement surgery, patients from two hospitals were compared in a retrospective study of matched samples. Patients participating in CAI used less oral pain medication than the control group (32).
- Patients with moderate or greater anxiety in an emergency room had lower anxiety following CAI than those in a control group (33).
- Patients with heart failure selected to walk with a dog had a lower ambulation refusal rate (7.2 vs. 28%) and achieved greater ambulatory distance than a historical sample not participating in CAI (34).
- Cancer patients participating in CAI during chemotherapy had greater reductions in depression and increased arterial oxygen saturation compared with a control group (35).

In addition to the benefits of CAI reported for patients, hospital healthcare professionals were also found to benefit from CAI in a pilot study documenting reduced physiological stress. Significant reductions in both serum and salivary cortisol were detected 45 min after 5 and 20 min of CAI (36). No cortisol differences were found between either treatment condition and 20 min of quiet rest suggesting that hospital staff may benefit from very brief CAI.

The promising evidence of CAI benefits for various hospital populations coupled with the low-cost of CAI programs utilizing community volunteer therapy dog teams support CAI as a feasible complementary intervention to traditional medicine. However, the vulnerability of hospital patients and unique environment of the hospital setting pose challenges to conducting CAI safely and effectively for patients, staff, dogs, and volunteers.

ISSUES AND CHALLENGES

Therapy dog visitation programs in hospitals present many potential issues and challenges stemming from multiple sources. **Figure 1** presents a depiction of how the hospital setting and the accompanying program processes and oversight may impact the handler-dog-patient (staff member or visitor) triad.

Hospital Setting

Hospitalization is stressful for patients and their families (37) and evidence suggests that staff may suffer from compassion fatigue or burnout which places patients at risk from errors, abuse, or neglect (38) and has the potential to exacerbate an already stressful environment. For example, stressed nurses are more likely to make errors, less likely to interact with patients (helping them to cope with their illness) or each other (creating an isolated and competitive work environment) (39). The hospital setting also tends to include stressors that impinge upon human and animal senses. Visually, hospitals may be crowded, with people moving about quickly, or include seriously injured or sick people who may move unexpectedly or with great urgency. Hospitals may be loud with irregular sound interruptions from overhead paging systems, beeping machines, or patients expressing pain or discomfort. There may be wide variety of strong odors including antiseptic or cleaning fluids, vomit, or burnt flesh. Surfaces in hospitals tend to be smooth, hard, or flat for easy cleanup or built for utility rather than comfort so the tactile experience is also not particularly relaxing. This variety of sensory experiences can be stressful and likely impacts on all three points of the triangle (e.g., dog, handler, patient) depicted in **Figure 1**.

Humans, including patients, staff, and visitors, may experience a variety of psychological and physiological stress reactions that are both acute and chronic in nature (40). Well-trained and temperament tested dogs who are newly placed into a hospital setting may become stressed and less responsive to their handlers. We will focus our discussion on each of the three aspects of the handler/dog/patient triad, but it is important to remember that many of these issues or challenges overlap with, and apply to, more than a single aspect on the triad.

Handler Concerns

Handlers are faced with a variety of potential challenges in hospital settings including routine practical issues such as what items to bring with them, where to park their car or exercise their dog, to more complex issues like how to safely avoid exposure to infectious diseases, and what topics of conversation are appropriate with each patient or visitor. In most, but not all cases, the dog handler is a person who is volunteering their time to bring their own dog to the hospital for visits. The handler has typically invested a sizeable amount of time and energy into training, testing, and registering their dog with an appropriate therapy dog organization (e.g., Pet Partners). Research on human–dog attachment has shown that attachment styles tend to mirror those found in mother–child relationships (41) and similarly influence stress coping, such that secure attachment tends to be associated with better stress coping. This may suggest

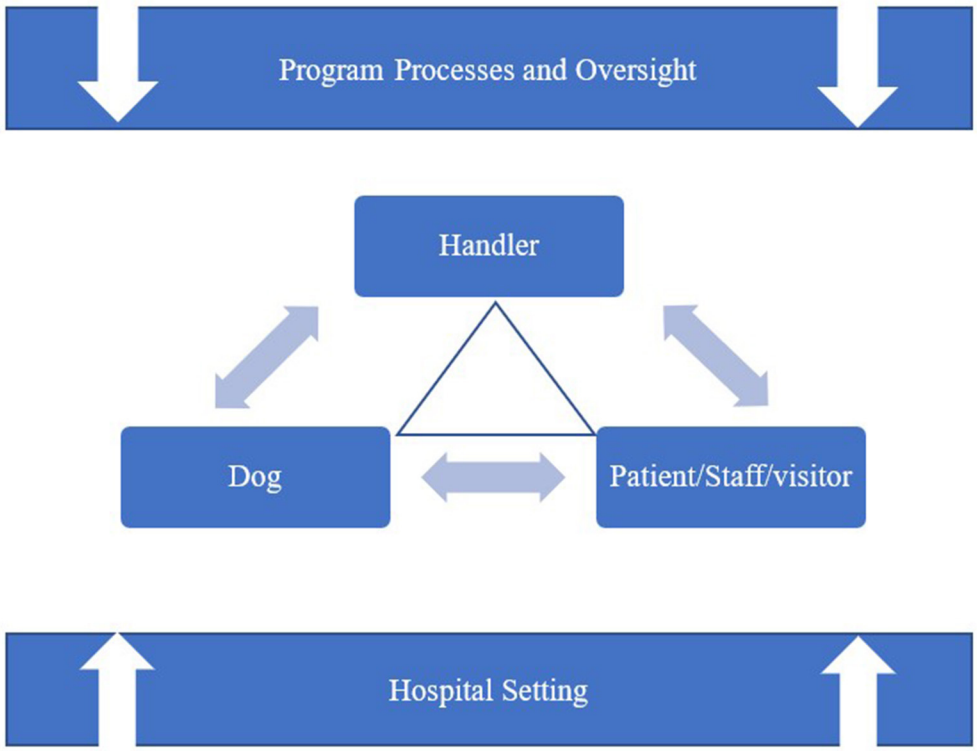

FIGURE 1 | Sources of potential issues and challenges.

that handlers with secure attachments to their dogs may more effectively cope with the wide variety of stressors in the situation.

Canine-assisted interventions (CAI) handlers often train their dogs to be in close proximity to, and interact with, strangers which appears to create behavioral adaptations during CAI, such that the dog may maintain greater eye contact with their handler as a way of maintaining contact during uncertainty (42). Attachment styles and behaviors indicative of maintaining contact during CAI are taken as additional indicators of the strength of the bond between the human and the animal. It is important to consider this bond as both a positive and a negative aspect of CAI because it is likely to influence handler behaviors and reactions during CAI. On the positive side, the bond between handler and dog may drive the handler to pay close attention to all things that may affect, or stress, their dog and act immediately to ensure the safety and well-being of their dog. It is critical to the safe practice of CAI to have a person in the environment whose role it is to focus exclusively on the health and well-being of the animal. They should be vigilant for things that might harm the dog, and for signs of stress or discomfort in the dog and act accordingly to protect the safety of the animal. On the negative side, a strong bond between handler and dog may contribute to handlers using poor judgment regarding their dog's behavior in the environment. For example, they may allow the dog to perform behaviors (e.g., certain tricks or off-leash walking) that the dog may enjoy, overlooking how safe or appropriate those things may be in that setting.

If a handler notices that their dog is stressed, their role is to remove the animal from the situation, but they are frequently confronted with opposing pressures to extend the visit. For example, the handler may see that a person is enjoying interacting with the dog, or the person may be in pain (emotional or physical) and taking great comfort from the dog, or the person may be alone and near the end of life and may simply want to touch the dog for a little longer. Handlers frequently struggle with what they may perceive as the morality of ending the visit under these more extreme circumstances. For this reason, it is important to prepare handlers for these challenging situations, give them tools to help them to deal with each individual situation appropriately, and provide ongoing support. Furthermore, there is some evidence to indicate that owners may not be well-prepared to recognize signs of stress in their dogs, and that they may benefit from educational efforts to improve their ability to recognize and interpret signs of stress in their own dog (43).

Like hospital personnel, handlers are subject to the stresses inherent in a hospital environment. Exposure to patients who are suffering, facing terminal illness, and who die during hospitalization may contribute to handler anxiety and stress and secondary traumatization. Handlers who regularly visit a service may see a patient several times and 1 day finds the patient gone. Since they do not have access to confidential patient information, handlers are left wondering about the status of the patient.

Unlike hospital personnel who can debrief with colleagues about patient conditions, including the death of a patient, and access employee assistance programs, handlers are left to process such situations alone unless support services are made available to them. Compassion fatigue is a risk for handlers that may lead to burnout, withdrawal from volunteering, or compromise their ability to safely provide CAI (20).

Canine Concerns

In an attempt to establish standards of welfare for livestock animals, the Brambell Report defined ideal states known as the Five *Freedoms* (44). These are freedom from (1) hunger and thirst, (2) discomfort, (3) pain, injury, or disease, (4) fear and distress, and (5) the freedom to express normal behaviors. The Five Freedoms have been widely accepted and adopted by many professional organizations (e.g., the American Veterinary Medical Association) across a wide array of research and applied settings. Sandoe and Christiansen (45) built on these fundamentals by attempting to define what might constitute a good animal life in which it is important to consider that animals have needs and preferences that may be different from those of humans. Another concept relevant to the inclusion of animals in human–animal interaction is that of *a life worth living* (46). This idea addresses the animal holistically over the course of their lifetime and is based on basic states, overall welfare, value of life, and quality of life. Related to the concepts of the Five Freedoms is the Five Domain Model which has been updated and revised over the past 20 years to incorporate scientific thinking into the assessment of animal welfare [for a review see (47)]. This model considers both negative and positive affective states or experiences, and explores concepts such as agency of the animals involved in human–animal interaction research and practice.

Because it is a human choice to include the dog in animal-assisted interventions, it is incumbent upon the humans to make sure that the dog is experiencing a life worth living, and the Five Freedoms provide a starting point for this discussion. When a dog enters a hospital setting it is critical that the dog is consistently well fed and hydrated, free from disease and parasites, calm, unstressed, and demonstrating behaviors indicative of comfort with people and the surrounding environment. The primary responsibility for ensuring these things falls to the handler, in collaboration with their veterinarian (for the dog's health and wellness), the therapy dog registering agency (e.g., Pet Partners, Alliance of Therapy Dogs), and local program administrators and evaluators.

A 2017 review of the existing evidence ($N = 17$ studies) indicated that the use of aversive training methods jeopardizes both the physical and mental health of dogs (48). A recent empirical investigation comparing positive (i.e., beneficial) methods to the use of a shock collar provided further evidence to support these conclusions. The study demonstrated that dogs trained with positive training techniques achieved better responses and shorter latencies to common commands (e.g., "sit" and "come") than the dogs in the aversive training condition (49). The authors conclude that positive training was more effective and posed fewer risks to dog welfare and the quality of the human–dog relationship.

Routine veterinary wellness exams, vaccinations, and fecal exams to check for internal parasites help handlers to monitor the health of their dogs and reduce the risk of zoonotic disease transmission between humans and dogs (e.g., rabies). The recent COVID-19 pandemic has highlighted the fact that it is not possible to completely eliminate the risk of disease transmission (e.g., a novel virus) among humans and dogs, but monitoring the ongoing health of both species can reduce the risk and allow for early detection and treatment of potential health issues.

Safe dog–human interactions require the understanding of dogs' signaling behaviors and there is a striking lack of knowledge of these behaviors in the general public (50). Shepherd (51) proposed a ladder of dog behaviors indicating escalating levels of distress. On the lower steps in the ladder the dog will demonstrate several appeasement and calming behaviors such as yawning and nose licking, turning their head or body away, and walking away. As they feel more stressed, they may pin their ears back, tuck their tail under their body, stand in a crouch, lying down, leg up. As they become distressed, the dog may stiffen their body and stare, growl, snap, and finally bite. It is critically important to the welfare of the dog, for handlers and program personnel to be able to identify low level signs of stress and to act immediately to remove the animal from the situation. Acting upon this knowledge can defuse a situation, make interactions more enjoyable for the dog, and create an environment that is more relaxed, enjoyable, and respectful of the unique contributions of the dogs.

There are many potential risks to dogs in a hospital setting, requiring the handler to be vigilant in monitoring their dog's safety. For example, something may have been dropped on the floor (e.g., medication) of a patient room or spilled (e.g., body fluids) in the hallway. Equipment can be both fragile and top heavy, so if it is inadvertently knocked over the dog may become injured. Equipment and people can block or crowd a pathway, creating obstacles that may be intimidating to the dog, requiring the handler to recognize and carefully navigate unexpected situations.

Patients can also be a source of risk to the dog. Some patients may have difficulty with gross or fine motor movements and may stumble onto the dog, or roughly grab at the dog. Other patients can become overly interactive with the dog and hug them tightly or attempt to pick them up or move them in ways the dog does not enjoy. Some patients will attempt to share their food or drinks with the dog. Children may pull their hair or tail, and I.V. bags and lines may startle the dog if they become entangled in them.

The handler carries a heavy responsibility in monitoring their dog, their interactions with humans, and any potential risks in the environment. It is important for the CAI program and hospital to provide education and support to handlers in carrying out these responsibilities.

Patient/Visitor/Staff Concerns

Patient and healthcare provider safety is a top priority for all healthcare facilities, including hospitals. Therapy dog presence represents a risk to that safety in the form of potential zoonotic

pathogen transmission, cross-transmission of human pathogens, injury, and symptom exacerbation.

Insufficient research has been conducted investigating the role of dogs as a vector for zoonotic disease transmission in hospitals (52). We were able to find no studies investigating therapy dogs and cross-transmission of human pathogens. One study examined hospital infection rate as a pilot CAI program was being implemented in an Italian pediatric hospital (53). The hospital's infection control committee independently monitored infection rates over a 12-month period. Although attendance at the weekly CAI was high, no increase in infection rate compared with the previous year was found.

Two recent surveys conducted in the United States examined CAI health and safety policies and practices. One study surveyed 45 hospitals, 45 senior care facilities, and 27 therapy dog organizations with results showing inconsistent policies to safeguard patient health and animal welfare (54). Particularly alarming, the survey found 70% of therapy dog organizations surveyed permitted dogs to be fed a raw meat diet. A nationally representative survey of U.S. therapy dog organization practices reported similar results of inconsistent practices that may risk human health and canine welfare (55). Results also revealed a concerning number of organizations failing to limit raw meat diets and treats and failing to place time limits on therapy dog visits.

Feeding a raw meat diet remains a contentious subject among some therapy dog owners. A study of salmonella and other potential pathogen risk in therapy dogs in Canada fed a raw meat diet found dogs fed raw meat at some point during the yearlong study were more likely to test positive for salmonella and extended-spectrum cephalosporinase than dogs not fed raw meat (56). No differences were found in associations between eating raw meat and *Clostridioides difficile*, methicillin-resistant *Staphylococcus aureus*, or vancomycin-resistant Enterococci.

In the absence of studies providing more conclusive evidence on the role of canines in zoonotic pathogen transmission and cross-transmission of human pathogens, strict infection prevention and control procedures, including the ability to contact trace CAI interactions, must be established for CAI to maximize patient, healthcare provider, and CAI team safety. Two recent publications address this issue and provide guidelines for the safe practice of CAI in hospitals (52, 57).

In addition to zoonotic disease transmission, therapy dogs represent a risk for injury to patients, visitors, and healthcare personnel as well as to other therapy dogs if providing CAI with other therapy dog teams. Although evaluated for health and temperament by therapy dog organizations to minimize such risk, dogs still have the potentially to trip, scratch, or bite someone in the environment or accidently interfere with equipment (e.g., knocking over equipment). Hospital policies and procedures must address such risks, provide direction for handling such incidents, consider liability issues, and develop procedures to minimize risks.

Dogs in the environment also present a concern for patients, visitors, and staff with allergies to canine dander and fear of dogs. CAI programs must address these potential risks to maximize human safety.

An additional potential issue for handlers, patients, and hospital personnel is the illness and/or death of a therapy dog. For the handler, serious illness or death of their therapy dog often represents a significant loss (58, 59). Not only have they lost a beloved canine family member, but unless they own more than one therapy dog, they also lose an important activity and the relationships and gratification associated with being a hospital volunteer and providing CAI. Processes are needed to support handlers at such times. Patients and personnel routinely visited by a therapy dog may also be saddened and grieve when a therapy dog becomes seriously ill or dies (60). Patient and staff support services need to be cognizant of the significance such incidents may pose and provide appropriate resources.

A less obvious issue for handlers and patients is the ability of therapy dog teams to meet the demand for CAI. Patients and staff requesting CAI may be disappointed if the visit does not materialize. This can be particularly difficult for pediatric patients who may be informed that a therapy dog will be coming or observe the CAI team visiting other patients and leaving the unit without seeing them. Staff training in understanding the limits of CAI resources and presenting the intervention as requested but not guaranteed can help minimize negative reactions when a requested visit cannot be fulfilled.

For CAI to be successful, hospital staff must understand basic information about the approved CAI program. Staff must be informed of areas approved for CAI, criteria for determining patient appropriateness to participate, and procedures to request CAI for their patients. An understanding of therapy dog and handler requirements to deliver CAI is important to maximize appropriateness of requests. Ideally key hospital administrators and staff are involved in the development and ongoing evaluation of any CAI program in their setting.

RECOMMENDATIONS FOR BEST PRACTICE

Best practice is defined by Merriam-Webster (61) as "a procedure that has been shown by research and experience to produce optimal results and that is established or proposed as a standard suitable for widespread adoption." Therefore, to be suitable for widespread hospital adoption, a CAI best practice program must be evidence-based and historically shown to produce recognized high-quality results with minimal negative effects. Such a program should be time-tested, address the canine, handler, patient, visitor, and staff concerns described in the previous sections, and be shown to be effective in the hospital setting. We present best practice recommendations with examples from a program model that meets these best practice criteria. The inclusion of experiential information related to the model program is unavoidably subjective.

Program Model: Dogs on Call

Dogs on Call is a therapy dog program established in the Center for Human–Animal Interaction at Virginia Commonwealth University (VCU) School of Medicine in 2001. The program model depicted in **Figure 2** forms the basis for the following

FIGURE 2 | Integrated best practices program model—Dogs on call.

discussion. Dogs on Call provides CAI throughout the VCU Medical Center and meets the criteria for Best Practice:

- proposed as a standard suitable for widespread adoption (57) and selected as a model healthcare CAI program featured globally by Mission Critical Health
- published efficacy studies providing evidence base
- time-tested intervention operating in a major academic medical center since 2001
- established 19-year history of safety for humans and canines.

Dogs on Call policies and procedures were developed in concert with internal representatives from diverse disciplines including epidemiology, veterinary, and human medicine, and healthcare administration as well as informed by relevant professional guidelines related to infection control, animal-assisted interventions, and animal welfare. Policies and procedures are reviewed and updated on a regular basis to reflect changes in hospital policies and procedures, new knowledge from relevant fields, and results of formal and informal evaluation efforts. The program is manualized to promote standardized interventions delivered throughout the medical center.

Dogs on Call requirements include documentation of external therapy dog registration (Pet Partners or Alliance of Therapy Dogs), completion of VCU Medical Center volunteer services training, completion of Dogs on Call training, and adherence to manualized policies and procedures. The owner/handler and dog are evaluated and approved to participate together as a dyad in CAI programs. The unique bond and communication between them contribute to the safe practice of CAI and attention to canine welfare. Biannual meetings are held to provide program updates, reinforce program fidelity, provide continuing education, and solicit feedback. Teams are evaluated individually at least biennially to monitor program fidelity. Handlers participate in ongoing CAI related continuing education in such areas as canine behavior, patient safety, responding to difficult requests, and compassion fatigue. Program efficacy is documented through ongoing research and evaluation, disseminated through professional publications and internal and external education, and utilized in making program revisions. For detailed information on the Dogs on Call program see Barker et al. (57), and visit the program website[1].

Best Practice Recommendation: Involve Hospital Administration and Staff

Any novel program being considered by a hospital has a higher chance of being established, continued, and successful with administrative and employee involvement and support. Establishing such relationships and ongoing awareness of relevant research and practice are important foundations for any CAI program. For example, the involvement of medical, nursing, legal, volunteer services, veterinary, and other medical center administrators in developing Dogs on Call program policies and procedures were key to the program's credibility, acceptance, and ongoing support as a medical center program. One avenue for facilitating such involvement is establishing CAI executive and/or advisory committees involving key high-level administrators to build a sense of ownership and oversight by the hospital. Whether the CAI program is internal as is Dogs on Call, or external as with visiting community-based CAI programs, such committees serve to facilitate communication between the CAI program and

[1]https://chai.vcu.edu/programs--services/dogs-on-call/

hospital employees at all levels. Establishing liaison relationships with key hospital staff on services targeted for CAI promotes coordination and feedback regarding CAI activities. Liaisons can facilitate CAI scheduling, establish any needed service-specific orientation (e.g., pediatrics, psychiatry) for handlers, and provide CAI teams with unit-level assistance and support. Building relationships with frontline staff increases the likelihood of staff comfort with the CAI program and willingness to contact the program with any concerns, questions, or requests. These liaisons also enhance the CAI program's ability to monitor program implementation and resolve potential problems. Patient conditions in the hospital can change very quickly making real-time screening of patient appropriateness by front-line clinical staff critical to patient safety. Staff knowledge of the CAI provides an important framework for making informed decisions in screening patients and gauging the milieu for appropriateness for CAI on any given day.

Best Practice Recommendation: Develop Informed Policies and Procedures

In addition to comprehensive knowledge of HAI and AAI, input from internal and external content experts representing other relevant disciplines is critical for developing policies and procedures to maximize therapy dog welfare and human safety in the hospital setting. At a minimum, representatives from human health (including epidemiology, medicine, and nursing), veterinary medicine, hospital risk management, hospital administration, and volunteer services should be involved. Their ongoing involvement provides a conduit for updating CAI policies and procedures based on evidence and regulatory changes from the diverse fields affecting a CAI program in a healthcare setting. For example, when COVID-19 cases began emerging in Virginia in March of 2020, Dog on Call operations were guided by the medical center's infection control department and hospital administration. Since Infection Control personnel and hospital leadership were knowledgeable of the Dogs on Call program, rapid infection control and visitation guidance was provided from an informed perspective of both Dogs on Call practices as well as COVID-19 risk to patients, CAI teams, and staff.

CAI policies and procedures are strengthened by incorporating relevant published guidelines. The publication of the Society for Healthcare Epidemiology of America guidelines for animals in health care facilities provides recommendations for service and therapy animals informed by science and current practice (52). A 2019 published manual for establishing and maintaining CAI in health care facilities represents another resource (57). Based on research and extensive experience, the manual includes recommendations on infection control reviewed by the Society for Healthcare Epidemiology of America.

It is important to note that at a minimum, most CAI programs require some type of handler-dog training and initial assessment to determine that minimum competencies are met. Therapy dog organizations providing such training and assessment vary in not only their initial requirements, but also requirements for renewal and their policies for members. Some renewals are payment-based with documentation of animal wellness while others require periodic re-evaluations of the dog/handler team. Such variability in requirements and policies highlight the need for hospitals to go beyond therapy dog organization requirements and develop comprehensive informed policies and procedures to maximize human and canine safety.

Policies and procedures should address CAI oversight as well. Identifying those responsible for the program establishes needed accountability and provides CAI handlers and hospital employees with individuals to contact with questions and concerns. In addition to monitoring therapy dog and handler ongoing compliance, oversight must include attention to canine welfare, and a system for monitoring where CAI is being conducted at any given time. This information will be needed in the event contact tracing is required. When a Dogs on Call handler thought his dog might have ringworm, he reported the incident to the hospital's Dogs on Call coordinator who immediately contacted Infection Control and contact tracing was initiated. Although the handler called later that day to confirm a veterinary consult ruled out ringworm (or any contagion), the contact system was able to be effectively initiated because CAI teams are monitored for time and location.

Oversight responsibility also includes addressing canine or handler problems or complaints that arise. Addressing any non-compliance with policies and procedures must be handled immediately for the safety of humans and canines and to ensure program integrity. For canine misbehavior, policies should detail clear steps to remediate the behavior (e.g., disruptive barking) or terminate program participation (e.g., any display of aggressive behavior). Oversight also includes implementing methods to acknowledge the contributions of CAI teams and to address ongoing recruitment and retention.

Best Practice Recommendation: Develop Ongoing Program Fidelity and Evaluation Strategies

The most rigorous and well-informed CAI policies and procedures can only be effective if implemented as intended. Ongoing evaluation is an important component of any successful program to maintain program integrity and assess program worth and effectiveness (62). Dogs on Call monitors program fidelity by monitoring team members completion of annual hospital-mandated volunteer requirements, compliance with Dogs on Call program requirements, and completion of biennial evaluations of each team. Biennial evaluations consist of observing the team as they perform CAI in the hospital to monitor compliance with policies and procedures, observe handler-canine communication, and monitor canine body language for signs of fatigue or distress.

Hospital administrators are more inclined to support and continue programs that are shown to be effective. Providing evidence of efficacy involves evaluation. In addition to informing decision-makers, evaluations can provide valuable information for improving CAI processes, determining which patients benefit from CAI and in what ways, and identifying resource needs.

For example, during the development of Dogs on Call, a needs assessment was electronically sent to all nursing coordinators in the hospital to determine interest in and concerns about a CAI program on their services. The results provided an indication of program demand, but just as importantly, identified areas for staff education on CAI to address their concerns. Ongoing studies of Dogs on Call have identified clinical populations benefiting from brief CAI (e.g., psychiatric, urology) (15, 30) as well as benefits for health care professionals (36). Such research also identified pediatric patient outcomes not significantly affected by CAI and unintended outcomes important for consideration in future research (e.g., low pediatric pretest distress and pain scores, use of pain medication) (25). Fidelity of implementation is critical for determining program reliability and efficacy. When delivery of CAI is not consistently conducted as intended, safety is jeopardized and results of any investigations are compromised.

Best Practice Recommendation: Prioritize Canine Welfare Considerations

Although primary responsibility for canine welfare resides with the therapy dog owner, hospitals must also share some of that responsibility when CAI is approved on their premises. Hospital administrators are uniquely qualified to identify potential safety issues for canines in their facilities and develop strategies to minimize risk. For example, VCU Medical Center recognized the potential danger that dropped medication poses for therapy dogs. They proactively involved Dogs on Call representation on their medication safety subcommittee addressing this issue. Dogs on Call team orientation emphasizes continuous handler surveillance of the environment for potential risks for their dogs, including dropped medications, fluids, and food.

In addition to addressing risks, CAI programs must emphasize canine wellness in their policies and procedures as well. CAI programs benefit from involving hospital administrators in addressing therapy dog welfare. Such collaboration facilitates identifying adequate parking to accommodate safely unloading dogs, designating adequate exercise, rest, and elimination areas, identifying on-site or local veterinary resources for emergent issues, and developing processes for CAI team check-in and check-out to enable contact tracing, not only for possible canine-to-human zoonotic transmission but human-to-canine transmission as well.

In setting firm time limits for dogs in the hospital, the CAI program can address a canine welfare issue inconsistently addressed by therapy animal registration organizations (55). Setting firm time limits (e.g., 2 h maximum) for the dog on the premises provides a program regulation to support canine welfare and provide handlers with an objective rationale for denying requests to lengthen time in the hospital.

It is important to emphasize canine welfare in CAI orientation and continuing education, including understanding canine body language and recognizing when the dog does not enjoy the environment. Some dogs may not be comfortable in highly stimulating settings (e.g., pediatrics, emergency departments) but are very comfortable in more predictable surroundings (e.g., adult services, outpatient clinics). Handlers become very invested in participating in CAI and may not recognize changes in their dogs over time that may indicate they are fatigued or no longer enjoying the hospital setting. Periodic monitoring of the therapy dog team by CAI program staff can assist with identifying when a dog may need a break or retirement from CAI. Continuing education for handlers normalizing retirement can be helpful, but in the end the CAI program must be willing to administratively retire a therapy dog if it is in the best interest of the dog.

SUMMARY AND PRACTICAL IMPLICATIONS

This paper began by summarizing the evidence supporting benefits of CAI in hospital settings while noting the existence of conflicting evidence and the need for further research. Several studies have documented positive results of CAI, but there is little consensus in the clinical populations studied, outcomes and measurements selected, and methodological rigor. The exceptions to these disparate positive findings are accumulated studies showing CAI benefits for cardiac and psychiatric patients.

To advance research on CAI in hospital settings, established CAI programs are needed. Yet the hospital setting presents unique challenges for the delivery of CAI. Sources of potential issues and challenges for humans and dogs involved in CAI in the hospital setting were presented based on the literature and the authors' extensive experience administering and conducting CAI. Best practice recommendations for CAI program processes and oversight were then provided with examples from a model best practice program operating in a major medical center.

Practical Considerations

For people interested in establishing a CAI program in a hospital setting, gaining entry may seem like a daunting task. Identifying one or more key allies in the hospital can facilitate this process and provide valuable guidance on preparing a proposal that has a higher likelihood of being accepted by administrators. Hospital employees likely represent the surrounding community and their opinions can provide insight into views regarding pet ownership and the potentially favorable impact of a CAI program. However, it would be a mistake to assume that hospital employees are aware of hospital-based CAI and evidence supporting benefits. Our initial needs assessment at VCU Medical Center revealed many misconceptions and concerns about therapy dogs in the environment, including that dogs would be dirty, noisy, and disruptive in the environment and bring fleas, ticks, and other sources of illness to patients. An initial educational approach to introducing CAI may lay the groundwork for acceptance and support of the program.

Ultimately approval, support, and endorsement of CAI at the highest administrative levels is desired, but the process of securing such widespread support takes time, planning, and patience. The antecedent of Dogs on Call was a small pilot project conducted by the first author on inpatient

psychiatry. Suggesting a pilot project as an entrée to CAI has advantages for those approving the project. "Pilot" implies temporary and therefore can be discontinued if the process and outcomes are not considered valuable or beneficial. Including an evaluation component can provide documented outcomes to support the program. Outcomes can include informal feedback from patients and staff and/or simple assessments measuring mood or anxiety. More than any other single factor, results documenting positive patient outcomes contributed to the growth in credibility and widespread support and institutional integration of Dogs on Call at VCU Medical Center.

Cost-effectiveness is a key consideration for hospitals considering any new program. A benefit of CAI is that therapy dogs reside with their owners in the community. Owners assume the costs of ownership including veterinary care, food, training, therapy dog registration, etc. They provide CAI as volunteers, incurring only a modest cost to the hospital for providing volunteer orientation and required training, vaccinations, and record-keeping. CAI programs need adequate funding to develop, implement, maintain, and evaluate the program. Identifying funding sources is challenging for CAI in any context with competing interests vying for a limited pool of financial resources. Successfully competing for funding against requests for healthcare and allied health personnel, equipment, patient needs, information technology, infrastructure and the myriad of other hospital needs is enhanced with evaluation data documenting the value of CAI in terms of benefits to patients, staff, and the organization.

Some programs, including Dogs on Call, establish themselves as non-profits eligible for tax-deductible donations and seek support from community foundations, grants, and individuals. Again, evaluation is key to demonstrate program efficacy to potential sponsors. Some CAI programs charge a nominal annual fee for membership and require members to purchase branded merchandise (shirts, dog vests) while others raise funds to provide membership and merchandise at no charge to members.

As the popularity of a CAI program grows, so does the demand for services. Recruiting, training, and monitoring additional CAI teams can strain existing program resources. Experiencing such demands, Dogs on Call developed a Leads Program to assist with these efforts. Experienced Dogs on Call members are recruited, educated, and trained to assist with recruiting and onboarding of new members and monitoring for program fidelity. Meeting regularly with Leads members enhances their program involvement, visibility, and recognition as senior level volunteers. Their experienced insights and feedback strengthen and inform program policies and procedures.

Conclusion

Canine-assisted interventions (CAI) have the potential to complement traditional medical treatments in contributing to the health of hospitalized individuals. The hospital setting presents unique challenges to humans, dogs, and dog handlers in providing CAI effectively and safely. Recommended best practices are presented based on the literature and a model best practice program to guide hospitals and CAI programs in implementing programs that maximize canine welfare and human safety. More evidence of CAI efficacy with hospitalized patients is needed. To advance existing research, studies must be undertaken utilizing rigorous methodologies to investigate CAI programs that meet best practice criteria.

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SB and NG conceived the idea for the paper together. SB provided the initial organization of the paper. All authors wrote the document in shared collaboration.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Commensalism or Cross-Species Adoption? A Critical Review of Theories of Wolf Domestication

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The work of archaeozoologists and molecular geneticists suggests that the domestication of the wolf (*Canis lupus*)—the ancestor of the domestic dog (*C. familiaris*)—probably occurred somewhere between 40,000 and 15,000 years ago somewhere on the Eurasian continent, perhaps in more than one location. Wolf domestication was therefore underway many millennia before the origins of agriculture and the domestication of food animals, such as sheep and goats. Currently, there are two predominant "origin stories" concerning the domestication of the wolf. The dominant narrative in recent literature is the *commensal scavenger* hypothesis which posits that wolves essentially domesticated themselves by invading ancient human settlements in search of animal remains and other edible waste discarded by hunter-gatherers. Over time, tolerance by humans gave a selective advantage to the bolder, less fearful wolves, which then diverged from the ancestral population as they adapted to the new scavenging niche. At some point in the process, humans also began to recognize the benefits of living with resident, semi-domestic wolves, either as guards or as hunting partners, thereby cementing the relationship. The alternative account of wolf domestication is very different. Sometimes known as the *pet keeping* or *cross-species adoption* hypothesis, this narrative draws heavily on anthropological observations of pet keeping among recent hunter-gatherers, and postulates that Paleolithic peoples were similarly inclined to capture, adopt and rear infant mammals, such as wolf pups, and that this habitual human nurturing behavior ultimately provided the basis for the evolution of a cooperative social system involving both species. This review critically examines and analyzes these two distinct domestication narratives and explores the underlying and sometimes erroneous assumptions they make about wolves, Pleistocene humans, and the original relationships that existed between the two species. The paper concludes that the commensal scavenger hypothesis is untenable based on what is known about recent and ancient hunter-gatherer societies, and that wolf domestication was predicated on the establishment of cooperative social relations between humans and wolves based on the early socialization of wolf pups.

Keywords: dogs, wolves, domestication, commensalism, pet keeping

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INTRODUCTION

Prior to the domestication of livestock animals—sheep, goats, pigs, cattle, horses, llamas, camels, poultry, and so on—all humans lived as subsistence hunters and gatherers who obtained their food directly from nature either by hunting, fishing, or foraging. As far as is known, humans lived like this for at least 2 million years (1) until the closing stages of the last major period of glaciation when, relatively suddenly, some communities in various regions of the world began the process of domesticating plants and animals. This relatively abrupt change from hunting and foraging to domestic food production was one of the most transformative episodes in the history of our species, and it is one that raises a variety of interesting questions. Why, for instance, did humans domesticate plants and animals when they did and not earlier or later, and why in only some geographic regions but not in others? Why also did they domesticate only a small subset of the numerous wild animal species that were potentially available to them, and why, given the many possible choices, did the entire process begin with a large and potentially dangerous carnivore, *Canis lupus*, rather than with something less intimidating and more obviously useful?

The purpose of the current review is to focus specifically on the last of these questions by critically examining the different competing accounts of how and why certain groups of late Pleistocene hunter-gatherers domesticated a large, group-living carnivore, the wolf, the ancestor of the domestic dog. The aim is to re-evaluate some of these different narratives to reveal the underlying assumptions they make about the nature of prehistoric humans and their relations with animals and the natural world.

The Origin(s) of the Dog

Archaeozoologists and paleogeneticists now suggest that the domestic dog was derived originally from Pleistocene wolves sometime between 40,000 and 15,000 years ago during the Last Glacial Maximum (LGM), possibly in more than one region of Europe and/or Asia (2–7). Wolves were therefore the first animals to be domesticated by humans, preceding the domestication of food or livestock species, such as sheep and goats, by a minimum of 4–5 thousand years. This fact alone raises important questions regarding the possible circumstances and motives leading late Pleistocene hunter-gatherers to single out the wolf for this unprecedented role. It is probably safe to assume that wolf domestication was originally unintentional since Paleolithic humans would have had no concept of the possible future benefits that might arise from such a novel association. At the time, wolves would have competed directly with human hunters for access to similar prey species (8), as well as posing a potential danger to any young or isolated humans who strayed too far from the protection of the group. As such, they would hardly seem an obvious candidate for domestication. Early humans may have hunted and killed wolves opportunistically as occasional sources of food or fur. However, they were never likely to have been a major target of subsistence hunting by Paleolithic peoples because apex predators such as wolves are necessarily less common and more dispersed than their prey (9). So why then did humans and wolves embark on such a risky and seemingly unproductive interspecies collaboration?

Unfortunately, because all of this occurred in prehistory, no written, pictorial, or oral records exist regarding what really happened or why. However, this has not deterred numerous authorities from offering speculative theories that purport to explain how and why our predecessors chose to share their lives and limited resources with this unlikely canine partner. Of these, two very different hypotheses currently dominate the debate, and will be the focus of the present review.

THE COMMENSAL SCAVENGER HYPOTHESIS

The currently dominant account of wolf domestication posits a world in which late Paleolithic or Mesolithic (Epipaleolithic) hunter-gatherers lived in seasonal hunting camps around which substantial quantities of garbage (animal carcasses and remains, human waste, and so on) accumulated. Attracted to this easy source of food, wolves began scrounging around the garbage dumps, first as occasional visitors and eventually, over time, as permanent or semi-permanent commensal scavengers. Early humans, in turn, tolerated these incursions and, as a result, over multiple generations, the wolves would have become gradually bolder and less fearful of people (10). Later, as the commensal association became more established, the humans would begin to notice the side-benefits of living in association with these animals, such as their tendency to alert to approaching danger or their superior powers of tracking and pursuing game. The humans might then have started giving preferential treatment (e.g., food, protection, etc.) to those individuals that demonstrated these useful traits to the greatest degree, thereby unconsciously initiating a process of artificial selection that resulted in gradual genetic divergence and, eventually, full domestication.

Several versions of this theory can be found in the scientific literature on dog domestication, all of which appear to originate from an imaginative fable first published in the opening chapter of Konrad Lorenz's popular book, *Man Meets Dog* (1953). Here, Lorenz depicts nomadic bands of human hunter-gatherers some 50,000 years ago whose successful hunting activities inevitably attracted the attentions of scavenging wild canids who then began to frequent their hunting camps in search of discarded bones, offal, and so on. After a time, the humans began to realize that, while the scavenging canines were a minor nuisance, they also provided a useful shield against larger marauding predators (e.g., saber-toothed tigers) by barking loudly whenever one was prowling in the vicinity. Now, instead of chasing the dogs away, the humans began encouraging them to remain nearby by actively provisioning them. And so, bit by bit, the process of domestication gathered steam:

> "Many years have passed, many generations. The jackals[1] have become tamer and bolder, and now surround the camps of man

[1]Lorenz believed erroneously that most modern dog breeds descended from the golden jackal (*Canis aureus*) rather than the wolf. Given the jackal's natural scavenging proclivities, this mistaken assumption may have contributed to his account of domestication.

> in larger packs …. Whereas, formerly they remained concealed by day and only ventured abroad by night, now the strongest and cleverest among them have become diurnal and follow the men on their hunting expeditions" [(11), p. 7].

Though rarely cited, Lorenz's account gained early support from several prominent archaeologists and anthropologists, some of whom argued that so-called "pariah" dogs, the ubiquitous canine scavengers of contemporary Asia, represent surviving relics of just such an early association between humans and wild canids (12, 13). More recent versions of the theory, usually attributed to (10), are also based on firsthand observations of so-called "village" or "dump" dogs—i.e., contemporary free-roaming dogs in parts of Africa and Latin America that exist primarily by scavenging from large municipal waste dumps in densely populated urban areas. Though less elaborate and fanciful, these recent versions of the scavenging hypothesis are nevertheless essentially no different in substance from Lorenz's original narrative. For example, an authoritative account published in the prestigious *Proceedings of the National Academy of Sciences* in 2009 states that:

> "Wolf domestication was initiated late in the Mesolithic when humans were nomadic hunter-gatherers. Those wolves less afraid of humans scavenged nomadic hunting camps and over time developed utility, initially as guards warning of approaching animals or other nomadic bands and soon thereafter as hunters" (14).

Similarly, an April 2015 edition of *Science Magazine* reported that:

> "Most experts now think dogs domesticated themselves. Early humans left piles of discarded carcasses at the edges of their campsites—a veritable feast, the thinking goes, for wolves that dared get close to people. Those wolves survived longer and produced more pups—a process that, generation by generation, yielded ever-bolder animals, until finally a wolf was eating out of a person's hand. Once our ancestors realized the utility of these animals, they initiated a second, more active phase of domestication, breeding early canines to be better hunters, herders, and guardians" (15).

Challenges to the Commensal Scavenger Hypothesis

Ecological Constraints

Though superficially plausible, this account of wolf domestication is not without its challengers. The eminent geographer, Sauer (16), for example, referred to this theory as "an attractive myth," and more recently, Jung and Pörtl (17) have strongly disputed the notion that late Pleistocene humans in Europe or Asia reliably generated enough carrion or waste to sustain a permanent population of scavenging wolves. Current evidence suggests that the wolf was already domesticated by the end of the Last Glacial Maximum (LGM) about 15 K years ago (kya) when humans still lived in the relatively small and highly dispersed nomadic groups associated with typical hunting and foraging societies (18). Estimates of human population size and density during this late Pleistocene period are necessarily somewhat speculative, but it is clear that northern hunter-gathers typically live at low or very low densities, proportional to the diversity and abundance of the principal mammalian prey species on which they depend (19). Based on habitable land area during the LGM, and data from 219 different extant hunter-gatherer groups worldwide, recent estimates of the total human population in the Old World (i.e., Africa, Europe, Asia, and Australasia combined) during this period range from 2 to 8 million people, living at densities of between 2 and 12 persons per 100 km^2 (20). Similarly, population estimates for the whole of Europe during the LGM suggest an average of fewer than 30 thousand individuals (21). Even allowing for the fact that these populations may have been more densely clustered in some areas than in others, this would appear to be insufficient to create a viable ecological niche to support a stable population of scavenging wolves; a species that is reported to need up to 6–7 lbs of high protein food per day in order to reproduce successfully (22).

In the past, advocates of the commensal scavenging hypothesis have argued that wolf domestication actually occurred sometime during the Epipaleolithic/Mesolithic 15–8 kya, despite archaeozoological and paleogenetic evidence to the contrary (13, 14). This period, at least in Europe, was associated with the first appearance of larger and more permanent human settlements, particularly in riverine and coastal areas, and correspondingly greater accumulations of trash or "middens," mostly consisting of the discarded shells of edible molluscs (23). This desire to place wolf domestication much later than the evidence suggests may reflect the difficulty of reconciling the scavenging hypothesis with the realities of Pleistocene (as opposed to Holocene) hunter-gatherer ecology. In short, human trash dumps and middens of the kind found in Epipaleolithic and Neolithic Europe may have provided limited scavenging opportunities for local carnivores, but they are much too recent to have contributed to wolf domestication.

The only possible exceptions to this rule are the substantial accumulations of predominantly mammoth bones and tusks associated with human activities at various sites in Central and Eastern Europe during the LGM between 40 and 24 kya. Some archaeologists have interpreted these sites as the unused and unwanted by-products of successful mammoth hunts which might indeed have provided important, if temporary, sources of edible carrion for foraging wolves. Other experts, however, have argued that these accumulations of bones and tusks were the result of the deliberate collection and storage of potential building material in regions of steppe tundra where wood for shelter construction was in short supply (23).

Cultural Constraints

The ecological problem of finding sufficient edible, organic waste to support a population of scavenging wolves would likely have been exacerbated by hunter-gatherer ritual practices associated with the disposal of the unused remains of hunted animals. Although little is known about the hunting beliefs and rituals of Pleistocene hunter-gatherers, their more recent counterparts are notoriously careful to avoid wasting unusable or inedible

portions of the animals they kill and are typically scrupulous about how they dispose of these unused remains (24–32). Referring to one Native American group in central Alaska, the anthropologist, Nelson (28), states that, "[O]ne of the pervasive themes in Koyukon ideology is a prohibition against wasting anything from nature. If someone kills an animal and then leaves it unused or neglects to return for its meat, bad luck or illness will come as punishment. Meat should be carefully butchered and cached where it will not spoil or be defiled by scavengers, and it should be used as fully as possible to avoid offending the animal's protective spirit." The desire to avoid defilement "by scavengers" is particularly apposite in the current context, suggesting that Paleolithic hunters might have been similarly reluctant to leave any animal remains lying around unused that might have attracted, let alone supported, groups of scavenging wolves.

Certainly, millions of free-roaming dogs currently occupy a commensal scavenging niche throughout much of the developing world (33, 34), so clearly the ability to survive on a diet of human garbage and waste has been an important contributor to the domestic dog's evolutionary success as a species (35). However, these large populations of roaming dogs tend to exist now in areas with long histories of cultural development, high or very high human population densities, and poor or nonexistent means of waste management (36). And even in these circumstances, high rates of adult and pup mortality mean that many free-roaming dog communities are barely sustainable without periodic recruitment from the owned dog population (33, 37). This implies that the scavenging niche is a relatively marginal one in which dogs typically struggle to survive and reproduce successfully without additional human provisioning. Overall, this would indicate that the appearance of permanent populations of canine scavengers was a relatively recent development in dog evolution which only became possible after the first emergence of large towns and pre-urban cities during the Neolithic period around 8,000 years ago, at least 7 thousand years after wolves were supposedly domesticated.

Safety Constraints

It is also pertinent to ask why Pleistocene humans would have been interested in tolerating or even encouraging wild wolves to frequent their hunting camps. Supporters of the commensal scavenger hypothesis tend to gloss over this question by assigning an essentially passive and disinterested role to the humans involved in the process. For example:

> "People create a new niche, the village. Some wolves invade the new niche and gain access to a new food source. Those wolves that can use the new niche are genetically predisposed to show less 'flight distance' than those that don't. Those 'tamer' wolves gain selective advantage in the new niche over the wilder ones" (10).

This summary account appears to conflate reduced 'flight distance' with true tameness when they are really two separate phenomena. A wild animal that tolerates close approach by humans before fleeing has either lost its fear through repeated, non-threatening exposure (i.e., habituation) or for some reason has never developed a fear response in the first place. An animal that has been tamed, in contrast, not only tolerates human contact but actively seeks it out due to the formation of social bonds. The theory of domestication based on commensal scavenging, at least in its early stages, does not involve tamed wolves—wolves that have been socialized with humans—but rather wild wolves that have habituated to the presence humans and which voluntarily approach and frequent human settlements to gain access to food. The recent history of human-wildlife interactions would suggest that such animals would pose a significant danger to humans, especially to the more vulnerable members of the community. As one pro-wolf website aptly advises:

> "when wild animals become habituated to people, they may lose their fear of humans, especially if they are fed or if they associate humans with providing food. Like any large predator, wolves are perfectly capable of killing people. No one should ever encourage a wolf or any other wild animal to approach, and hikers and campers should take all necessary precautions to prevent mishaps involving wildlife" (22).

Attacks on humans by wolves and other wild canids are nowadays unusual, but certainly not unheard of (38). Between 1987 and 2000, five separate attacks on humans by four different, healthy, adult wolves occurred in Algonquin Provincial Park in Canada. In each case, the wolves involved had been frequenting recreational campgrounds where they had received handouts from campers for weeks or months beforehand and had lost their fear of humans (39). Similarly, a much-publicized fatal attack by a pair of coyotes (*Canis l. latrans*) on a lone female hiker in Cape Breton Highlands National Park in Nova Scotia, Canada, in 2009 was linked to long-term habituation and provisioning of local coyotes by tourists. On Fraser Island, Australia, some 279 negative, human-dingo interactions were reported to local authorities between 1996 and 2001 of which 40 were classified as major or catastrophic. The single catastrophic incident involved the killing of a 9-year-old boy and severe mauling of his 7-year-old brother by a pair of habituated dingoes (*Canis f. dingo*). Subsequent analyses determined that habituation of wild dingoes through deliberate or inadvertent feeding by tourists was the foundation for the vast majority of these predatory interactions (40).

Such incidents also appear have been more common in the past, and often in the absence of accidental or deliberate provisioning. An historical review of reported fatal wolf attacks on humans in northern Italy between the fifteenth and nineteenth centuries identified some 600 cases of humans being killed by non-rabid wolves, most of the victims being children under the age of twelve (41). Similarly, careful analysis of French historical archives has unearthed records of more than 3,000 fatal wolf attacks, particularly on women and children, between the fifteenth and twentieth centuries, mostly by healthy (non-rabid) wolves (42). In light of these kinds of evidence, it seems highly improbable that Pleistocene hunter-gatherers would have been comfortable with the chronic proximity of

habituated and fearless, scavenging wolves, regardless of their early warning potential.

THE CROSS-SPECIES ADOPTION (OR PET KEEPING) HYPOTHESIS

The other competing account of wolf domestication involves the deliberate capture, adoption, hand-rearing, and socialization of wild wolf pups by Pleistocene humans. The original version of this theory was first proposed in 1865 by Charles Darwin's half-cousin, Francis Galton, a Victorian polymath best known for his pioneering work in statistics, meteorology, psychometrics, and eugenics. On the topic of animal domestication Galton wrote:

> "It is a fact familiar to all travelers, that savages frequently capture young animals of various kinds, and rear them as favorites, and sell or present them as curiosities. Human nature is generally akin: savages may be brutal, but they are not on that account devoid of our taste for taming and caressing young animals; nay, it is not improbable that some races may possess it in a more marked degree than ourselves" (43).

Setting aside his disparaging depiction of indigenous cultures, Galton's point is that people should not make the mistake of assuming that pet keeping is something that is necessarily restricted to more developed, urbanized societies, but that it may actually be widespread and even more popular among those cultures that urbane Victorians regarded as primitive or "savage." To reinforce this point, he then went on to provide a lengthy catalog of reports from various noted explorers of the period describing cases of indigenous peoples all over the known world catching, taming and caring for young mammals of various kinds, and keeping them as pets. From here, in Galton's view, it was a matter of common sense to infer that similar pet keeping practices must have existed in prehistoric times and would have led to the eventual domestication of those species that naturally possessed certain characteristics of temperament and behavior that predisposed them to domestic life. These traits, he argued, included hardiness, a tendency to seek comfort or safety, usefulness to humans, a willingness to breed in captivity, tractability ("easy to tend"), and what he referred to as "a fondness for man," an apparent reference to the animal's ability to form social attachments to humans, for otherwise it would, in his words, "fret itself to death, or escape and revert to wildness."

Thus, individual wild animal pets that failed to express such traits, or which expressed them only to a limited degree, would have tended to either die of neglect, wander off, or be driven away once they matured past the stage of being appealing as objects of nurturance. Conversely, those in which the traits were more developed would have received favored treatment, been more likely to reproduce as a result and, consequently, been more likely to pass on their desirable domestic traits to their descendants. (43)did not argue that these animals needed to be immediately useful in an economic or practical sense in order to be cared for by humans, though he acknowledged that economic utility would have contributed to their ongoing popularity over time. Instead, he focused on the uniquely human penchant for acquiring and nurturing young animals which, in his opinion, was the essential key to unlocking the doors to domestication.

Objections to the Cross-Species Adoption Hypothesis

Geographic Issues

One general objection to the cross-species adoption hypothesis, first expressed by the anthropologist, Downs (13), was that, while pet keeping is extremely widespread among recent hunting and gathering and horticultural peoples, domestication appears to have been very localized, at least in its early stages. If Paleolithic pet keeping gave rise to domestication, why then, he asks, didn't the two phenomena coincide everywhere? One obvious response to this critique was provided by Galton's (43) original idea—later expanded by Diamond (44)—that not all wild species are equally pre-adapted to domestic life to begin with. If this view is correct, then the geographically localized "hearths of domestication" (16) may simply have been those that happened to support the species of animals that were already pre-adapted to this role and therefore easiest to domesticate.

Additionally, the practice of pet keeping may itself have been localized in prehistoric times. Wholesale cross-species adoption seems to be a uniquely human activity that rarely occurs naturally in other mammals outside of captivity [see (9, 45)]. It must therefore have developed as a cultural characteristic at some point in human evolution, perhaps just prior to the first domestication of wolves. Unfortunately, archaeological evidence of ancient pet keeping is understandably scarce, but there are early indications that wolves, dogs and other canids were sometimes the objects of human admiration and affection. For example, in a burial site at Uyun-al-Hammam in Jordan dating from 17 to 14 kya, archaeologists discovered the well-preserved remains of a fox (*Vulpes vulpes*) that had been buried with two humans. The unusual circumstances of this burial led the authors to conclude that, "rather than the fox being treated as a 'grave good' it had a special relationship (i.e., companion) to the humans in these graves" (46). Similarly, some of the earliest archaeological remains of confirmed domestic dogs from later Paleolithic and early Neolithic sites in Europe, Asia and North America were also buried deliberately, either in individual graves or together with humans, in a manner suggesting that these animals were held in high regard by whoever buried them (26, 47, 48). One of these animals even displayed evidence of careful nurturing by humans prior to its death. Recent forensic analysis of dental pathology in a juvenile dog buried with its human owners at the 14 kya site of Bonn-Oberkassel in Germany has revealed that it experienced several debilitating episodes of severe disease, consistent with infection with morbillivirus (distemper), for at least 6 weeks before it died (49). Since morbillivirus infection is typically highly lethal in wild and free-roaming canids, the study authors suggest that this individual could not have survived for as long as it did without, "lasting and intensive human care," and that this provides, "the earliest known evidence for a purely emotion-driven human-dog interaction" (49). Such findings suggest that at least some late Pleistocene hunter-gatherers, like their more recent counterparts, occasionally developed strong emotional

attachments for their canine companions independent of the animals' practical utility or lack thereof.

A further possibility is that only a small subset of Pleistocene hunter-gatherers possessed the necessary incentive to domesticate their pet wolves. An illustration of this point is perhaps provided by the traditional relationships that existed between Aborigines and wild dingoes (*C. f. dingo*) in Australia. According to numerous historical and contemporary accounts, Aboriginal groups in Australia habitually captured and tamed dingo pups and kept them as cherished pets. In most cases, however, these tamed wild dogs were poorly provisioned and undernourished, and usually wandered off and reverted to the wild as adults (50, 51). This situation has raised questions among anthropologists as to why the Aborigines never domesticated—or re-domesticated—the dingo. In the context of the current discussion, however, it seems more appropriate to ask what incentive the Aborigines had to take their relationships with dingoes to this level. Young dingoes were clearly appreciated both as pets and as guardians, particularly among Aboriginal women. Occasionally they also participated in hunting expeditions but seem to have been of marginal practical value in this respect. All of these functions, however, could be provided simply by adopting and rearing new dingo pups from the wild. There was no reason for the Aborigines to retain these animals as adults, particularly given their voracious appetite and tendency to steal food from under the noses of their human partners (51).

In other words, the evolutionary transition from pet wolf to domestic proto-dog may have required an environment that could overcome this obstacle to domestication by providing both humans and their pet wolves with long-term access to sufficient caloric resources to allow both species to survive and reproduce while living together in a combined social group. Interestingly, this type of situation may have existed in some parts of Europe and Asia during the LGM. According to recent estimates, the major mammalian prey assemblages that existed across Northern Europe and Asia during the LGM—and on which both wolves and humans subsisted—would have provided human hunter-gatherers with a surplus of animal protein, particularly during the harsh winter months when plant-based calories would be less available. Unlike wolves, humans are only able to digest about 20% of their energy needs from protein, so any excess could have been fed to pet wolves without depriving humans of nutritional resources. Thus, people and their pet wolves would not have been in competition with each other for limited food resources, thereby enabling them to coexist over multiple generations; long enough to give rise to genetically isolated, breeding populations of proto-dogs (8).

Wolves Make Terrible Pets

A more specific objection to the pet keeping narrative focuses on the technical feasibility of taming wolves, or at least taming them to the point where they would be safe to cohabit as pets with human families. In all social mammals, including wolves, there is a short "sensitive period" in early development during which the young form their primary social relationships and attachments (52, 53). Among wolf pups reared under natural conditions this developmental window is relatively narrow, from roughly 1 to 3 weeks of age, thereby ensuring that the pups form their primary social attachments with just their littermates, parents, and other immediate family or pack members (54, 55). After 3 weeks of age, social attraction to unfamiliar individuals is rapidly replaced by social avoidance and fear and, by 5–6 weeks, it becomes increasingly difficult for them to establish social bonds with new partners. Adult wolves can also be socialized and tamed, but the process involves many months of isolation and careful habituation, and the effects may not be extended reliably to other unfamiliar humans (55, 56). As a consequence, modern attempts to produce wolves that are reliably willing to accept humans as social partners have necessitated removing pups from their mothers before 3 weeks of age when they are virtually blind and not yet weaned, and then bottle-feeding them until they are able to properly digest solid food. Even then, these animals often retain temperament traits as adults that make them somewhat difficult and demanding companions, at least in a modern context (10, 57). Such facts have led some authorities to conclude that the whole idea of Paleolithic humans capturing and keeping young wolves as pets is a romantic fantasy (10).

Such sweeping conclusions, however, seem unwarranted based on the evidence. For one thing, it is possible, or even probable, that the temperamental characteristics of Pleistocene wolves made them more amenable to domestic life than their recent equivalents. Due to their history of predation on livestock animals, the modern wolves of Europe and Asia are the products of thousands of years of intensive human persecution (58), so it would not be surprising if they have developed heightened wariness and reactivity in the presence of humans. Additionally, the kinds of temperament traits that render tame wolves unsuitable as pets in modern, urban situations—e.g., escaping and roaming, neophobia, fear of strangers, lack of trainability, predation of domestic livestock, and so on—would have been far less disruptive in a Paleolithic hunter-gatherer context where pet wolves would have lived unrestrained in small temporary settlements, miles away from the nearest unfamiliar human being. Furthermore, we know from numerous first-hand accounts that recent hunter-gatherers not only capture and hand-rear wolves and other wild canids successfully, but also breast-feed the pups that are not yet weaned (9, 51, 59–61). And even if breast-feeding is excluded, adequate human socialization of wolf pups may have been achieved in ancient times simply by removing young pups from the den temporarily and handling them intensively on a regular basis. For example, during a trip to the Alaskan interior in the late eighteenth century, the explorer and naturalist, Samuel Hearne, made the following observation of interactions between wolves and local Indians:

> "They always burrow underground to bring forth their young, and though it is natural to suppose them very fierce at those time, yet I have frequently seen the Indians go to their dens and take out the young ones and play with them. I never knew a Northern Indian hurt one of them: on the contrary, they always put them carefully into the den again; and I have sometimes seen them paint the faces of the young wolves with vermillion, or red ochre" [(62), p. 803].

From an evolutionary perspective, it is certainly reasonable to question why hunter-gatherers would visit wolf dens just for the pleasure of playing with the pups, or why they would go to the trouble of hand-rearing and sometimes breast-feeding such pups when they were unlikely to derive any immediate practical or economic benefit from doing so. A possible response to this question would be to argue that cross-species adoption, like intraspecies adoption, is simply a by-product of an evolved propensity for alloparenting and cooperative child-care in the human species that sometimes finds outlets in the adoption and care of unrelated—including non-conspecific—infants (63–66). While such parenting "mistakes" could entail minor evolutionary costs depending on the level of care provided, these might not outweigh the immediate psychological rewards of pet keeping, or the potentially greater inclusive fitness costs incurred by being too discriminating about the allocation of alloparental resources (67).

DISCUSSION

There are a number of key differences between the two accounts of wolf domestication reviewed in this article. First, in the commensal scavenger scenario, wolves essentially domesticate themselves by voluntarily occupying an ecological niche unwittingly provided by humans. Humans are depicted as playing an essentially passive role in the process; simply tolerating adult wolves in their vicinity until they eventually recognize practical uses for them, such as guarding, hunting, or waste management. As indicated above, a number of fundamental ecological, cultural, and safety constraints render this scenario highly unlikely when viewed from the perspective of Ice Age humans, and the theory also drastically underestimates hunter-gatherer knowledge of, and interest in, socializing and caring for animal pets, including large carnivores such as wolves (43, 60).

In contrast, the cross-species adoption story portrays humans as the primary agents of domestication; deliberately removing young wolf pups from the den and hand-rearing them as dependents. Over time, most of these early pets would have grown up and gradually reverted to the wild, but a small minority—those possessing the most socially desirable traits, such as tameability, trainability, and a tendency to affiliate with humans—might have received favored treatment and hence been more likely to have given rise to domestic descendants with similar characteristics. The final transition from wolves as pets to wolves as domestic proto-dogs may also have required a period of access to surplus animal protein in order to overcome competition for food resources between humans and their adult pet wolves.

The primary appeal of this second narrative is that it is consistent with the frequently observed pet keeping behavior of recent and contemporary hunter-gatherers, while also providing a way around two of the main objections to the commensal scavenger hypothesis: namely, the hunter-gatherer aversion to discarding unused animal remains, and the notion that early humans would have tolerated "fearless" but otherwise unsocialized wolves prowling around their settlements. Pet wolves socialized with humans from an early age would likely have been viewed as dependent group members eligible to partake in shared food resources, at least until they reached adulthood and could fend for themselves. And due to their early socialization experience with humans of all ages, they would not have posed the kind of physical danger to young or vulnerable individuals that is evidently associated with adult wolves that have been merely habituated. On the contrary, their primary affinity with their human foster families would have manifested itself in a motivation to actively defend the group from external threats.

The main weakness of this hypothesis is that it is based largely on observations of recent hunter-gatherer societies which may or may not represent good models of the animal-related attitudes and behavior of their Pleistocene equivalents. Pending the discovery of novel archaeological insights, the only way to address this concern is to point to the obvious ecological similarities between recent and ancient hunting and foraging societies, and the remarkable degree of consistency in animal-related attitudes and beliefs that exists among contemporary hunter-gatherer groups from widely separated regions of the world (25, 27, 68, 69).

A further strength of the cross-species adoption idea is its capacity to explain the transition to economically valuable working partnerships between humans and their earliest proto-dogs. With the exception of scavenging, nearly all of the practical uses and functions of domestic dogs that have given them added value throughout human history, including all the many variations on companionship, hunting, herding, protection, and transport, are predicated on the existence of amicable and cooperative social bonds with humans; social bonds that require early and intensive socialization with people (or their livestock) to be effective and enduring. In contrast, the commensal scavenging idea postulates the development of a human-canine relationship based primarily on habituation—the loss of fearful and avoidant responses—which, on its own, would not have provided a satisfactory basis for the kinds of cooperative working relationships that typify post-Paleolithic human-dog interactions.

Additionally, the commensal scavenger idea is specific to opportunistic carnivores and omnivores that can exploit carrion as a food source and it cannot be easily generalized to explain the domestication of most other species domesticated by Epipaleolithic and Neolithic humans, such as sheep, goats, cattle, buffalo, horses, asses, camels, llamas, alpacas, chickens, turkeys, rabbits, guinea pigs, and so on. The cross-species adoption hypothesis, in contrast, provides a universal mechanism for assimilating otherwise wild animals into the human social milieu; an essential first step in the domestication process (70).

Ultimately, the domestication of the wolf was probably a rare and extraordinary product of unusually optimal ecological conditions in some areas of Eurasia that permitted one or more groups of Pleistocene hunter-gatherers and their pet wolves to coexist and coevolve over multiple generations due to a temporary superabundance of animal protein. Once this relationship was firmly cemented, and wolves were living and breeding entirely within the human domain,

unconscious selection for dog-like behavioral traits would probably have been very rapid and increasingly irreversible. The unprecedented animal-human relationship that emerged from this process spread rapidly throughout the human population of the world and has since survived and diversified over tens of thousands of years. In the process, it has doubtless affected the cultural and evolutionary trajectory of our own species in fundamental ways. As with every new technology, the acquisition of dogs extended human senses and capabilities in novel ways, and probably contributed more than tangentially to the post-Paleolithic success of our own species.

CONCLUSIONS

The popular hypothesis that the domestication of the dog from the wolf originated from a commensal scavenging relationship between wolves and Pleistocene hunter-gatherers is untenable for several reasons. Human populations during the Last Glacial Maximum were too small, too dispersed, and too nomadic to reliably generate sufficient edible waste to sustain a specialized population of scavenging wolves. Hunter-gatherer ritual prohibitions against discarding or wasting the remains of hunted animals would likely have further limited wild wolves' access to anthropogenic food sources, while the potential dangers posed by habituated but unsocialized wolves would have discouraged Paleolithic hunters from allowing these animals to approach or frequent their settlements in search of food. Instead, the theory that wolf domestication emerged from the common hunter-gatherer practice of adopting young wild animals and keeping them as cherished pets presents a viable alternative route to wolf domestication. Wolf pups adequately socialized and perhaps breast-fed would not have posed a significant threat to the humans with whom they were familiar and, as adopted family members, would have been provisioned and cared for until old enough to fend for themselves. While the majority were doubtless encouraged to revert to the wild as adults, a small minority, especially those displaying the most dog-like and appealing social behavior, might have been retained through to sexual maturity, perhaps aided by ecological conditions favoring reduced competition with humans for food. Once these pets were able to live out their entire lives with their human foster groups and produce surviving offspring with similar affiliative traits, the stage was set for full domestication and unconscious human selection for other advantageous behavioral variants. Thus, pet keeping, a commonplace hunter-gatherer leisure activity probably derived from alloparenting, accidentally gave birth to a biologically unique and unprecedented human-animal relationship which spread rapidly across human cultures throughout the world.

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OPINION
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Considering the "Dog" in Dog–Human Interaction

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Keywords: human-animal interaction, dog-human interaction, welfare, animal use, experience, point of view, consent

HIGHLIGHTS

- A focus on the experience of the silent partner in dog–human interaction research: the dog.
- Developing a vocabulary to discuss not just the welfare of the dog but also their perspective and agency.
- Raising issues about use of non-human partners, for the species, and for individual members of that species.

INTRODUCTION

The lives of the contemporary human animal and other non-human animals are surprisingly antithetical. While one might imagine that our mutual membership in the animal kingdom would predicate reciprocal interactions, we instead have a largely imbalanced relationship with non-human animals (hereinafter, "animals"), with animals bearing the brunt of this imbalance. People eat animals for nourishment or enjoyment, keep animals captive for meat or as pets, cage animals for amusement, use animals as models for studying human disorder and disease, and kill animals for sport, for being a nuisance, or for being inconvenient. Even the research fields of animal behavior and animal cognition are not entirely exempt from this imbalance. Animal cognition, borne of comparative psychology, largely studies animals to determine how they reflect on human cognition; animal behavior research studies animals for their own sake, but often that research involves interfering with, maiming, or killing the animal in the course of research. Some widespread human behavior, such as keeping animals as pets in the home, does evince an interest in other animals, but it is worth remembering that this is a model of animal captivity, which also produces millions of homeless or unmanageable animals who are killed annually in the United States alone (1).

In this context, the field of human–animal interaction (HAI), which avows an interest in the salutary effect of interacting with animals, seems an anomaly. On examination, though, it appears to be another example of the antithetical approach that typifies our other engagements with animals. In all cases, animals are *used* by humans. In HAI research, the animal is a quiet partner, useful only for the effect their presence has on the person, and rarely considered in and of themselves. Such research is likely performed in large part by individuals who deeply care about animals, human or not; as a result, they may be able to take the lead in imagining how the non-human animal could also become the subject. In this opinion piece, I highlight the consideration of animals in HAI research and suggest some ways to foreground the animals so used.

While HAI is defined broadly to include myriad forms of interaction between the human and non-human animal, I will focus on dog-human interaction research as exemplary of HAI research in its breadth and aims. The great preponderance of this work investigates the effects on people of various characterizations (elderly, children, developmentally different) of various interventions or interactions with dogs. Dogs are a convenient species to work with, as they have long been domesticated: bred to feature traits and behaviors that appeal to us, such as their

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friendliness, adaptability to interspecific living, and attention to our attention (2, 3). Dogs are tractable, easily trained, and widely available. Many dog–human interaction studies investigate the interactions between dogs and their present owners, obviating the researchers' needs even to house or train animals.

Most dog–human interaction studies investigate whether a specified exposure to a dog is salutary to humans (4). The common-sensical notion that animals who are already inside our homes "must" be good for human health implicitly or explicitly drives this research. Research has looked at mental health (such as reducing stress), physical health (such as decreasing rates of asthma, obesity, and lowering blood pressure), and general socioemotional benefits [e.g., McCardle et al. (5)]. However, there is no unanimous consensus about the benefits of therapies for humans involving animals; results are equivocal [(6, 7); for a review of the kinds of results over the last decade, see Griffin et al. (8)].

In contrast to the myriad forms and number of studies on the effect for humans on the interaction, very few studies, relatively, gauge the effect—either short- or long-term—on the dogs involved (9–11). As of 2017, Glenk found just nine HAI studies in peer-reviewed journals considering the effect of the work on the dog. These studies attempted to measure the dog's welfare when participating in therapeutic situations known as animal-assisted interventions, animal-assisted therapy, or animal-assisted activity. Search terms by Glenk (10) reveal several additional published journal articles in the 3 years since her publication. While these additional papers represent a small fraction of the research published in these years on HAI, the idea that dog welfare is integral to the programs is clearly spreading. Recent studies use different methods of characterizing welfare, from physiological measures like heart rate and cortisol levels (12–17), to behavioral measures of stress, like panting, lip licking, and yawning (14, 16–18), which may partially explain why there are, overall, mixed results.

Another possibility for the mixed results is the great differences in the dogs themselves. Considering all individual dogs, across breeds, age, sex, temperament, personal history, and health, as representative "dogs" is characteristic of this work as published. Their status is operationalized: dogs are treated less as subjects than as stimuli. They are typically not described as subjects or participants; they are thus, by default, objects. Who they are as individuals is rarely acknowledged in published work. Examining how the dogs are described in papers on HAI research, we get a sense of their negligible status. As Griffin et al. (8) note, most studies have no information on even very basic demographics of the dogs, such as sex, age, breed, desexing status, or training history. Even in the research designed to investigate the welfare of dogs in HAI work, who the dogs are is often underspecified. At best, sex, breed, age, health, living situation, weight, and source of dog, if known, is reported (19–21), although these figures may be averaged. In other work, neither individual breed nor sex information is given, nor is any life history (22, 23). A few papers with single subjects do better, such as Piva (24), which describes not only the typical demographics of the dog, but her personality with people, her testing temperament, her skill at performative obedience, and additional physical features.

This deficit is analogous to the report of animals kept—and the conditions in which they are kept—in most scientific work, historically. As Adams (25) notes about Ivan Pavlov's research, for instance, though it is widely cited, and clearly represented as involving dogs, no details of the dogs, such as the length of their lives, the conditions (social, living) of their lives, the procedures done to them, or even how their lives ended, are included either by Pavlov or by the textbook authors or journal papers that cite the research.

Only rarely are dogs named in the published reports of these studies [see Clark et al. (12), for a single instance]. The longstanding prohibition against naming animal subjects in behavioral science was famously flouted (if inadvertently) to great effect by Jane Goodall (26); since then, though animals might be named by researchers, they are still infrequently named in reports of the research results (whether researchers included the names in submitted manuscripts or not). Naming makes something someone: it personalizes them (27). To give an animal a name highlights the differences between subjects (individuals) being considered only as members of a group (species). In a postscript to his paper, Adams (25) lists the names of some of Pavlov's dogs, as a way to begin to remedy their oversight. By not naming dogs, researchers demonstrate that they are not considering dogs as individuals at all; they are simply thought of as representative "dogs." It is perhaps no wonder, then, that their well-being is not being examined: only individuals can have well- or ill-being at all.

What do these observations about the status of dogs in HAI research highlight? Significantly, they highlight that our society supports animals being used—used for the sake of another: the human animal (4). Can using animals for our purposes be justified? One hundred years ago, it did not seem roundly exploitative to keep animals in cages for research by humans—for the sake of human health, curiosity, or anything else. As much as societal opinion about such uses has changed since that time, one wonders whether considering animals as only the material with which to look at our own health is similarly exploitative (or will look exploitative in another century). Even in HAI research (with dogs, but also with horses and other domestic animals) in which the humans involved consider the animals their "partners" or "companions," the study subject is mostly one-sided.

"Use" need not necessarily mean "exploitation": to not exploit, but merely use animals, one must make choices that further the welfare of the animal, even if it is in conflict with one's motives (28). This definition prompts the further question of whether the very process of domestication, as traditionally conceived of Clutton-Brock (29), and breeding—focally redesigning a species to suit our whims—might be seen as exploitative. There certainly have been deleterious results for many domesticated animals: they have become largely food products, their natural life cycle and their normal social behavior disrupted. While domestic animals kept as pets do, in some cases, enjoy freedom from many of the pressures of living independently of humans, and are often

loved (whether the expression thereof is beneficial for them or not), they are constitutionally "captive" (30).[1]

While not expecting HAI researchers to solve the global question of animal use, within the field there is much room to mitigate the problems associated with use. I consider a few below: beginning to see, through identification and description, the animals involved in research; working toward positive welfare for animal participants; and appreciation and formal acknowledgment of the animal experience.

Who Is the Dog?

While on its face it does not sound disparaging or incomplete, in HAI work, dogs are just "dogs." What they are not are: subjects, agents, individuals, sentient participants. Not only their names, but basic facts about each dog's biology, behavior, and personalities are often completely absent from reports of research critically involving them. In considering animals in science, Birke (31) discusses a group of research animals seen as "numbers, as tools of the trade," "whose experiences are considered unimportant": she is referring to lab animals. We assume that the experience of dogs in HAI research far surpasses that of dogs living their lives in laboratories—but that's just the point: without the research, we can only assume. We will make mistakes about their experience if we do not even look. We need to begin to see the dogs in the research. Who are they? What are their histories; what are their preferences; what are their personalities? Indeed, it is because of their personalities that dogs are valued for much HAI work: so can we describe them? Use without identity promotes the ongoing inequity, the "moral discontinuity" that not only is one kind of life more valuable but also that only one kind of life deserves to be seen (25, 31).

A Good Life

As seen above, there is an increasing volume of work aiming to identify markers of stress and anxiety in dogs in intervention and interaction settings. In other words, this research looks to identify whether there are any negative effects for dogs. Recently revised standards for work with dogs in animal assisted interventions lay out guidelines to ensure the "health, welfare, and well-being of dogs," aimed to avoid poor welfare: for instance, that "least restrictive, minimally aversive" training methods are used (32). But the absence of poor welfare does not imply the presence of positive welfare (33). The increasing volume of work on the ethics of animal use and on animal welfare is apt; the next step is to determine what interactions *improve* animals' health and well-being—which are salutary and appropriate for the individual animal. Dogs' positive welfare should itself be a focus of investigation [as it is beginning to be in other contexts: for instance, 4 of the 22 behaviors looked at in a recent study on child–dog interactions are markers of positive welfare (34)].

[1]A current debate asks whether dogs were exclusively domesticated by humans or whether wolves essentially "self-domesticated" into proto-dogs, insofar as there may have been self-selection by ancient wolves before selective breeding by humans began thousands of years ago. In either event, the result is that dogs are considered "domesticated," and the process of human selection is several 1000 years old.

Societally, in the last two centuries we have seen legislated concerns for animal well-being in the form of animal cruelty laws (in the US); notably, though, such laws only deal with truly gross disruptions of needs and well-being, such as killing or torturing [and even those are permitted if deemed "necessary" (27)]. Recent research has begun to address what animals not only need, but want (35–37); such standards should be applied not only to the most egregious cases of animal use, such as invasive laboratory experimentation, but to all animal uses.

Relatedly, currently best-practice recommendations for HAI research emphasize the importance of using animals who are appropriate and appropriately trained for the work; monitoring of their welfare during the work; and allowing for retirement of an animal from work (6, 32). At the same time, animals need to be "controllable" (38), to be polite, "not regularly vocalize inappropriately" (32), and to react (unnaturally) calmly to arousing stimuli. We could ask whether such work curtails an animal's full expression of a natural life (39), flourishing at whatever "sort of thing" the animal is (40): the dog's capacity for dogness (27). The biological needs and desires of non-humans are not identical to human needs (41), so advancing their welfare requires an understanding of the dog's perspective—an understanding that has hardly begun to be pursued in any field.

To begin, we can imagine that a good life for dogs includes not only freedom from suffering and establishment of general bodily integrity and well-being, but stimulation of the senses, an ability to run around; chances to do new things or familiar activities; dog and person companionship and physical interaction; to engage with the natural world, sniffing and rolling; and to have some control over their days and environment. Opportunities for play, joy, amusement, attachment, choice, exploration, and periods of rest are all salient. There is moral work yet to be done to ensure that the animals' health and well-being is prioritized.

The Dog's Point of View

Imagining the lived reality of a working or therapy dog's experience is critical to an understanding of what their needs might be. Like most owned companion dogs, dogs used in therapy have few choices but to go along with their owner or handler. While proper training and selection for dogs used in therapy settings usefully exposes them to, broadly, unfamiliar and various social and sensory situations, our imagination about the dogs' experience may limit our ability to anticipate their experience in a working setting. For instance, human unfamiliarity with the dog's strongly olfactory rendering of the world means that few attempts are made to predict or account for new smells associated with new settings and people. Odors are not experienced at the same rate as light is: smells emit from sources but need to be closely examined or to travel on air currents in order to be perceived, unlike seen objects, which just "appear" at once before our eyes, if there is no obstruction (3). Thus, the pace at which one might explore—and "see"—a new olfactory environment might be different than a new visual environment. Sound lands differently on dog ears than on human ears, given their proximity to the reflective surface of the ground; moreover, they are sensitive to higher frequencies than our ears

can detect, enabling perception of ultrasonic sounds produced by rodents or insects in the environment (42); vocalizations of children, often shrill, are less anticipatable by a dog than by a human conspecific (38). Dogs are often used exactly to be touched; while dogs vary in their endurance of stressful touching, such as hugs or head pats, even in the best cases this is a demand on the dog (3, 38).

A Modest Proposal: Asking for Consent

Perhaps most fundamental to considering dogs in HAI research is a clear delineation of the role of the dogs. If they are subjects, they should be thoroughly described, and the effect of the work not only in the short term, but also in the long term, should be investigated. Moreover, more work should be *designed* to specifically gauge their welfare, rather than assessing it as an afterthought. Welfare should include not only a lack of negative effects, such as an increase in stress levels, but also an increase in positive effects. While most work on the welfare of dogs involved in HAI research does the former, almost none does the latter.

By neither considering welfare assessment as integral to research, or even describing who the dogs are, most HAI research is using dogs as objects only. We can question whether this is justifiable with a sentient animal. Ought dogs, or any animal, be used to attempt to improve the lives of humans? One possibility might be to continue to allow use, but insist on consent—consent of the dogs to their participation. As sentient animals, dogs are, whether bred for work or not, experiencing their lives. They have preferences and emotions. Despite their selection for compatibility with humans, dogs are likely to show stress behaviors—as many handlers are already seeing (43). Use of dogs might be permitted if they are able to "opt in" and "opt out" of being so used, just as a human participant in research can give or withdraw consent. Insofar as the research examines the human–animal bond, voluntary participation is an essential element of a bond-like relationship (44).

Determining consent is not as tricky as it might seem with non-language-using animals. Many dog trainers have encouraged straightforward consent training, wherein dogs are taught behaviors they can employ to agree to participation in a medical procedure, for instance. Having a choice is a way to grant animals agency, central to good welfare (45). Additionally, human handlers or experimenters can be better trained to read body language of dogs that indicates that a dog agrees to participation, is simply enduring participation, or would rather not participate. Meints et al. (46), for instance, recently demonstrated not only how erroneous peoples' reading of dog behavior is, but how readily people can learn to correctly interpret dog signals. Still, validated standards of consent would lift this requirement out of individuals' judgments to a societal level. Just as human participants must give consent for participation for research to be conducted and published, having animal participants consent could eventually be required for publication of research involving them.

CONCLUSION

Ultimately, though joined to us by a hyphen, the animal in the "human–animal" interaction is largely neglected in published research. With a contemporary, and scientifically validated, understanding of animals such as dogs as sentient, their role must be seriously considered. In particular, I recommend that researchers and handlers be mindful of the animals' perspectives of the activities they are engaging in; strive not just for lack of poor welfare but also the presence of positive welfare; and work toward standards of affirmative consent. Some of this work could be aided by publishing concerns, which typically require summary information about animals: journal editors might, instead, emphasize the importance of specific information about individual participants, as well as encouraging consent. Today, dogs are too often operationalized in HAI research, rather than seen as individuals with experiences—whose experience ought to be foregrounded.

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REVIEW
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Enhancing the Selection and Performance of Working Dogs

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Dogs perform a variety of integral roles in our society, engaging in work ranging from assistance (e.g., service dogs, guide dogs) and therapy to detection (e.g., search-and-rescue dogs, explosive detection dogs) and protection (e.g., military and law enforcement dogs). However, success in these roles, which requires dogs to meet challenging behavioral criteria and to undergo extensive training, is far from guaranteed. Therefore, enhancing the selection process is critical for the effectiveness and efficiency of working dog programs and has the potential to optimize how resources are invested in these programs, increase the number of available working dogs, and improve working dog welfare. In this paper, we review two main approaches for achieving this goal: (1) developing selection tests and criteria that can efficiently and effectively identify ideal candidates from the overall pool of candidate dogs, and (2) developing approaches to enhance performance, both at the individual and population level, via improvements in rearing, training, and breeding. We summarize key findings from the empirical literature regarding best practices for assessing, selecting, and improving working dogs, and conclude with future steps and recommendations for working dog organizations, breeders, trainers, and researchers.

Keywords: assistance dogs, canine, detection dogs, selection, temperament, working dogs, protection dogs

Since their domestication more than 10,000 years ago (1–3), the nature of dogs' interactions with people has taken many forms. On one end of the spectrum, free-ranging dogs live largely on the outskirts of society, interacting minimally with humans other than to scavenge for food (4). On the other end of the spectrum, pet dogs are welcomed into our homes (5) and beds (6), valued for their companionship, and can evoke emotional reactions analogous to those in the parent-child bond (7–9). Within this patchwork of human-dog interconnectedness, working dogs represent a small subset of the dog population, but one that can have profound effects on human health and well-being.

The roles that working dogs perform, now and throughout history, have been extremely diverse. Dogs have played critical roles in hunting and agriculture [e.g., livestock guarding dogs, herding dogs; (10)], transportation [e.g., sled dogs; (11)], public health [e.g., medical detection dogs; (12)], and environmental protection [e.g., conservation dogs; (13, 14)]. Although dogs working in each of these areas provide important benefits to humans, a comprehensive review of the many roles that working dogs fulfill is beyond the scope of the current paper. Thus, in this review, we focus on working dogs employed in three of the most common applications: assistance, protection, and detection dogs.

The primary purpose of an assistance dog is to perform tasks for an individual with a disability that ultimately allows that person to achieve greater independence. Research suggests that these dogs are effective not only as mobility aids, but may also provide psychosocial benefits to their partners (15–25). Assistance dogs represent a more recently-developed working dog role (26). While the first assistance dog organization was established in the United States with the opening of The Seeing Eye guide dog school in 1929, assistance dog use became more widespread only as recently as 1990 (27), when the Americans with Disabilities Act protected the right of a service dog to accompany their partner to public places (28). As of 2020, there are 133 assistance dog providers accredited by Assistance Dogs International, Inc.[1] There are several distinct categories of placements that fall under the umbrella of "assistance dogs": guide dogs, who assist blind or visually impaired handlers with navigation of their environment; hearing dogs, who assist people who are deaf or hard of hearing by alerting to relevant sounds (27), and service dogs, who assist people with physical disabilities by helping with daily tasks such as opening doors and retrieving objects. In more recent years, service dogs have also been trained to assist people with Autism Spectrum Disorder (ASD) under the supervision of a third party, usually a parent (29), to assist Veterans suffering from posttraumatic stress disorder (30), and to use olfaction to alert their handler to relevant medical events (31).

In contrast to assistance dogs, the title therapy dog is often given to dogs trained to help people in other settings ranging from facilitating children's practice reading (32), to promoting social interactions among the elderly (33), or participating in psychosocial interventions for children with disabilities (34). While therapy dogs often provide directed services for a human handler, they do not have legally protected access to accompany their owner/handler into businesses and public places (35). Some therapy dogs are further distinguished from assistance dogs, as described above, in that their handler may not be the direct beneficiary of the dog's presence, but rather a facilitator of the dog's interactions with others, often in a health care or school setting. These therapy dogs may participate in animal-assisted interventions, a broad category of tasks which can refer to either animal-assisted therapy—undertaken in conjunction with a health professional, working toward a specific goal—or animal-assisted activity—undertaken in conjunction with a professional or volunteer in a more spontaneous setting (36). Although therapy dogs play important roles, this topic has been covered in depth elsewhere [e.g., (37, 38)], and so the current paper focuses solely on assistance, protection, and detection dogs.

Reports of using dogs for protection can be found as early as 700 BC, but the advent of modern police dogs only dates back to the early 20th century (39). Police dogs are used in law enforcement to aid in the apprehension of suspects, deterrence of crime, securing of points of entry, and locating of people or substances of interest. Similarly, the military trains single-purpose patrol dogs to scout, search buildings, and use controlled aggression. In addition, single-purpose detection dogs serve to locate explosives, narcotics, contraband, pests, and many more odors [e.g., (40, 41)]. Many law enforcement agencies and the military also rely on dual-purpose dogs who are used for both protection and detection. Search-and-rescue dogs are trained to find either live humans or human remains and can be trained for response in urban disaster settings or wide-area wilderness settings (42).

Thus, from helping people with disabilities safely and confidently navigate their environment to aiding in the safeguarding of our communities, working dogs provide numerous benefits at both the individual and societal level. They not only fulfill these key needs—often outperforming technologies designed for the same purposes—but they also enhance the lives of the people with whom they work through the human-animal bond (18, 43, 44). However, the process of identifying and training dogs with potential for success in these roles presents many challenges.

SOURCING OF DOGS

The first hurdle is determining how to source the dogs. There are several common models, all of which have their own advantages and disadvantages. Many assistance dog organizations (45) as well as some military dog organizations [e.g., the Swedish Armed Forces; (46)] maintain their own breeding programs, which is beneficial for several reasons. Breeding decisions can be informed by generations of information, affording organizations greater control over the health and characteristics of their dogs. For example, Guiding Eyes for the Blind reports that, through selective breeding, they have decreased the rates of hip and elbow dysplasia in their population by over 90% in the past 30 years (47). Also, organizations with their own breeding programs report the highest success rates for dogs from their own breeding programs (48, 49). However, dogs still need to occasionally be brought in from outside sources to maintain genetic diversity. Furthermore, breeding programs can be costly. One approach to improve success in breeding programs is to adopt a cooperative approach in which dogs who are suited for other careers are exchanged with complementary organizations (50).

The traditional approach to sourcing dogs for search and rescue is a community-based model (51). In this setting, individuals identify a dog with the potential physical and behavioral characteristics appropriate for a search dog (52). This individual approach may include identifying breeders with a history of success or simply a trial-and-error approach with individual dogs. This approach is labor intensive for the

[1]https://assistancedogsinternational.org.

individual and results in a variable success rate. Recently, some organizations have established programs in which trained search dogs from select breedings are available for pairing with handlers (e.g., Penn Vet Working Dog Center, Maranatha Kennels).

Another option which has great public appeal is to identify dogs from shelters or rescues to be trained as working dogs (51). This approach serves the double purpose of fulfilling a working need and providing a home to a dog. In theory, it represents a lower cost model, given that organizations are not responsible for the breeding and rearing of candidate dogs. However, this model has several challenges with identifying and training dogs to become successful working dogs. While medical conditions are (usually) readily screened, behavioral potential is difficult to evaluate (53, 54). Furthermore, dogs are often placed in shelters or rescues due to behavioral problems (e.g., fear associated with the environment or people, resource guarding, dog- or human-directed aggression) that are unsuitable for working dogs (55, 56). Although some programs have been successful in this approach, the financial investment can be greater than that for a breeding program or other acquisition approaches, especially if the organization maintains responsibility for adopted dogs who do not meet the working dog requirements. Thus, utilization of shelter and rescue dogs is best seen as a complementary approach until improved screening can be developed to clearly identify candidates that possess the physical and behavioral traits to be successful in a specific working career.

Finally, many smaller assistance dog organizations purchase dogs (57), and it is also common for the military to procure dogs from overseas (58). When acquiring dogs, the organization has the advantage of selecting only dogs who meet the physical and behavioral requirements, but current behavioral tests are imperfect and still result in a sizable proportion of dogs being subsequently rejected for behavioral reasons (57).

ATTRITION FROM TRAINING

An additional obstacle is that, even after undergoing rigorous selection and training, large numbers of dogs who enter training fail to complete these programs, largely for behavioral reasons (59–61). The consequences of unsuccessful dogs are numerous. Often, dogs are not deemed unsuitable until a year or two of age, at which point large amounts of time and money have already been invested in them. It is estimated that around 50–70% of assistance dogs are ultimately released from professional training programs (62), and the release rate can be as high as 80% for dogs acquired from a shelter (63). In addition to improvements in resource allocation, increasing the success rate of dogs in training also has welfare implications (64). For example, dogs bred for placement in protection roles often have characteristics, such as high motivation (sometimes referred to as "drive"), reactivity, and energy levels, that make them difficult to keep as pets. Similarly, accurate identification of dogs who are unlikely to succeed in working roles can eliminate potentially stressful transitions that these dogs would otherwise face (e.g., beginning a professional training program only to be rehomed shortly after initiation of this process).

To address these challenges, we advocate multiple avenues by which to improve the process of producing effective and healthy working dogs, that can ultimately lead to the placement of more dogs with a greater potential for success and welfare in these roles. We summarize key findings from the empirical literature regarding best practices for assessing, selecting, and improving working dogs, and conclude with future steps and recommendations for working dog organizations, breeders, trainers, and researchers.

WHAT FACTORS WILL OPTIMIZE THE PROCESS OF PLACING SUCCESSFUL WORKING DOGS?

Assessment and Selection of Working Dogs

One opportunity to optimize the production of working dogs occurs at the stage of deciding which dogs to train for working roles. The goal here is to refine and improve predictions of which dogs will ultimately complete training, and beyond that, thrive throughout long and productive careers. In practice, these evaluations can act as tools for information-gathering across relevant domains, but how they are applied and the subsequent cost-benefit analyses will vary based on the specific industry, the size of a given organization, the age at which training starts, and the origin of the dogs (e.g., from a breeding colony, private breeder, shelter). Importantly, implementation of these tests and criteria are meant to identify suitable candidates and thereby make selection more efficient, but would not result in improvement to the overall pool of dogs from which future candidates could be selected. Ideally, the selection process would take into account multiple factors that affect a dog's working ability, including various facets of the dog's behavior and cognition, early environment, and preferences. Below, we highlight factors linked to success, as indicated by prior research, in each of these areas.

Behavioral Considerations

Behavior is a major factor when it comes to placing working dogs. Accordingly, there has been a large research focus on determining which specific elements of canine behavior are necessary, and which are disruptive, when it comes to the ability of working dogs to perform their roles. Several reviews have been written about this topic in recent years, including an assessment of the behavioral tests used to select assistance, protection, and detection dogs (65), as well as other papers summarizing the behavioral and cognitive features believed to be important in the selection of detection dogs specifically (66–68). Additionally, studies have documented the qualities deemed most important for detection dogs by their handlers and trainers (69, 70).

In **Table 1**, we summarize 33 empirical studies that have assessed behavior in candidate (ages 3 months to 4 years) and active (ages 2.5–11 years) working dogs in order to determine associations with a work-related outcome. In addition to focusing on participants of a specified age range (i.e., 3 months and older) and with a reported outcome associated with a specified

TABLE 1 | Associations between behavior and outcomes in adolescent and adult candidate working dogs.

Paper	Authors	Year	Reference	Outcome	Breeds	Age at assessment	*n*	Measurement type	Behavioral traits related to outcome (direction of association with success)
a	Goddard and Beilharz	1983	(49)	Assistance: guide dog qualification	LR and GR	12–18 months	887	Ratings by trainers (of behavior over 3 weeks)	Fearfulness (–), distraction (–), aggression (–)
b	Wilsson and Sundgren	1997	(71)	Assistance: guide dog qualification	LR and GSD	450–600 days	2,107	Behavioral assessment	Ability to cooperate (+), courage (+, GSD only), nerve stability (+, GSD only)
c	Batt et al.	2008	(72)	Assistance: guide dog qualification	LR and GR	6 and 14–20 months	43	Behavioral assessment	Shorter latency to drop during passive test (+), greater latency to rest during passive test (+), absence of jumping during dog distraction task (+), higher lateralization index during tape test (+), lower rate of both paw usage during Kong test (+), lack of pulling during dog distraction task (+)
d	Arata et al.	2010	(73)	Assistance: guide dog qualification	LR	15 months	144	Ratings by trainers (of behavior over 3 months)	Distraction (–), docility (+)
e	Tomkins et al.	2011	(74)	Assistance: guide dog qualification	LR, GR, and LGX	13–17 months	113	Behavioral assessment	Panting and licking during dog distraction test (–), latency to sit in noise test (–), time resting in evening kennel (+)
f	Tomkins et al.	2012	(75)	Assistance: guide dog qualification	LR, GR, and LGX	13–17 months	114	Behavioral assessment	Right-directional paw preference in Kong test (+), strength of laterality bias in first-stepping test (+)
g	Harvey et al.	2016	(76)	Assistance: guide dog qualification	LR and LGX	5 and 8 months	93	Behavioral assessment	Time oriented toward food (–), shaking behavior after body sensitivity tests (+), lip licking (–), obedience in command-following (+), reactivity (–), distraction (–), Fear/anxiety (–)
h	Harvey et al.	2017	(77)	Assistance: guide dog qualification	LR, GR, LGX, and GSD	5, 8, and 12 months	1,401	Ratings by training supervisors (of behavior over months)	Trainability (+), distractibility (–), general anxiety (–), adaptability (+), excitability (–), stair anxiety (–), body sensitivity (–)
i	Bray et al.	2017	(78)	Assistance: guide dog qualification	LR, GR, LGX, and GSD	14–17 months	98	Behavioral assessment	Problem-solving performance (+), quicker to vocalize during a novel object task (–)
j	Cleghern et al.	2018	(79)	Assistance: guide dog qualification	LR	12 and 16 months	1,561	Ratings by puppy raisers (of behavior over months, at 12 months) and behavioral assessment (at 16 months)	Aggression toward unfamiliar people (–), fearful behavior (–), nervous on stairs (–), dog aggression (–), kennel anxiety (–)
k	Duffy and Serpell	2012	(62)	Assistance: guide and service dog qualification	LR, GR, LGX, and GSD	6 and 12 months	7,696	Ratings by puppy raisers (of behavior over months)	27/36 CBARQ traits, including pulling on the leash (–), energy level (–), hyperactivity (–), fear (–), and chasing (–)
l	Dollion et al.	2019	(80)	Assistance: guide and service dog qualification	LR, BMD, LBX, SP, RP, GR, and LGX	6 and 12 months	5,340	Ratings by foster families (of behavior over months, at 6 + 12 months) and behavioral assessment (at 12 months)	Fear/reactivity (–)
m	Berns et al.	2017	(81)	Assistance: service dog qualification	LR, GR, and LGX	17–21 months	49	Awake fMRI	Caudate activity (+) and amygdala activity (–) while watching hand signals
n	MacLean and Hare	2018	(82)	Assistance: service dog qualification	LR, GR, and LGX	2 years	232	Behavioral assessment	Human-directed gazing during unsolvable and social referencing tasks (+), inferential reasoning (+)
o	Bray et al.	2019	(83)	Assistance: service dog qualification	LR, GR, and LGX	12 months	3,569	Ratings by puppy raisers (of behavior over months)	Barking (–), stranger-directed fear (–), dog-directed aggression (–), coprophagia (+), trainability (+)

(Continued)

TABLE 1 | Continued

Paper	Authors	Year	Reference	Outcome	Breeds	Age at assessment	*n*	Measurement type	Behavioral traits related to outcome (direction of association with success)
o	Bray et al.	2019	(83)	Assistance: service dog qualification	LR, GR, and LGX	18 months	5,967	Behavioral assessment	Body tension during physical exam (–), reactivity during noise test (–), uncomfortable around unfamiliar dog stimulus (–), reactivity during prey test (–)
p	Weiss	2002	(63)	Assistance: trainer rating on "service success" scale	Varied	6 months–2 years	40	Behavioral assessment	High levels of vertical activity level when alone in an empty room for 4 min (–), trying to solicit interaction with a silent staring human (+)
q	Maejima et al.	2007	(84)	Detection: drug detection dog qualification	LR	1–2 years	197	Behavioral assessment	Desire for work (+): concentration, interest in target, obedience training, general activity, anxiety
r	Rooney et al.	2007	(85)	Detection: explosive detection dog trainer assessment of overall ability	LR	14–15 months	26	Behavioral assessment	Subjective measure of general search ability (+), free search thoroughness (+), location ability (+), systematic search behavior (+)
s	McGarrity et al.	2016	(86)	Detection: TSA odor-detection dog qualification	LR, V, and crosses	3, 6, 9, and 12 months	52	Behavioral assessment	Environmental stability: responsiveness (+), initiative (+), confidence (+), concentration (+); dominant possession (+); increase in hunt drive over 1st year of life (+)
t	Hare et al.	2018	(87)	Detection: search-and-rescue dog FEMA-certification	GSD, LR, GR, and assorted other breeds	1–11 years	129	Ratings by handlers (of behavior over months)	Fear of dogs (–), separation-related problems (–)
n	MacLean and Hare	2018	(82)	Detection: detection dog success	LR	4 years	312	Behavioral assessment	Sensitivity to human gesture cues (+), short-term memory (+)
u	Lazarowski et al.	2018	(88)	Detection: vapor wake® detection dog and explosive detection dog placement	LR and GWPX	3, 6, 10, and 12 months	146	Behavioral assessment	Performance (+): hunt, focus, possession, independence, work effort; environmental soundness (+): comfortable around surfaces, people, vehicles, quick recovery to visual startle, quick recovery to acoustic startle; trainability (+)
v	Lazarowski et al.	2019	(89)	Detection: detection dog qualification	LR and GWPX	3, 6, and 11 months	77	Behavioral assessment	Follow olfactory vs. deceptive social cues (+)
w	Lazarowski et al.	2019	(90)	Detection: detection dog qualification	LR and GWPX	3, 6, and 11 months	81	Behavioral assessment	Human-directed gazing during an unsolvable task (+)
x	Lazarowski et al.	2020	(91)	Detection: detection dog qualification and trainer evaluation of performance measures	LR and GWPX	3, 6, and 11 months	113	Behavioral assessment	Longer latencies to detour during first reversal trial of detour task at 3 months (+), more correct choices in acquisition phase of detour task at 11 months (+), short-term memory at 3 months (+)
y	Ganitskaya et al.	2020	(92)	Detection: speed of drug detection	LR, GR, ECS, RS, and GS	2.5–7.5 years	74	Behavioral assessment	Play (+), sociability (+), activity (+)
z	Tiira et al.	2020	(93)	Detection: police explosive search dogs annual search test success	BM, GSD, and LR	12–112 months	23	Behavioral assessment	Motor inhibition measured via cylinder task performance (+)
A	Svartberg	2002	(94)	Protection/detection: working dog trial performance	GSD and BT	12–18 months	2,655	Behavioral assessment	Boldness (+): playfulness, curiosity/fearlessness, chase-proneness, and sociability
B	Sinn et al.	2010	(58)	Protection/detection: military working dog dual-certification	GSD, BM, and DS	1–3 years	1,000	Behavioral assessment	Search focus (+), sharpness (+)
C	Wilsson and Sinn	2012	(46)	Protection/detection: Swedish Armed Forces training program success	GSD	15–18 months	496	Behavioral assessment	Engagement (+), confidence (+)

(Continued)

TABLE 1 | Continued

Paper	Authors	Year	Reference	Outcome	Breeds	Age at assessment	*n*	Measurement type	Behavioral traits related to outcome (direction of association with success)
D	Foyer et al.	2014	(95)	Protection/detection: military working dog suitability test (*T*-test) success	GSD	14 months	71	Ratings by puppy raisers (of behavior over months)	Trainability (+), hyperactivity/restlessness (+), chasing/following shadows (+), stranger-directed fear (−), non-social fear (−), dog-directed fear (−), touch sensitivity (−)
E	Foyer et al.	2016	(96)	Protection/detection: military working dog approval for further training as decided by suitability test (*T*-test) leader	GSD	15–19 months	85	Behavioral assessment	Ambivalent and overt fear-related behavior (+)
F	Brady et al.	2018	(61)	Protection/detection: military working dogs and police dogs long-term success	GSD, LR, ESS, BM, DH, and crosses	4–5 years	79	Ratings by handlers (of behavior over months)	Responsiveness (+), energy and interest (+)
b	Wilsson and Sundgren	1997	(71)	Protection: police dog qualification	LR and GSD	450–600 days	2,107	Behavioral assessment	Courage (+), hardness (+), prey drive (+), defense drive (+), nerve stability (+)
G	Slabbert and Odendaal	1999	(97)	Protection: police patrol dog qualification	GSD	6 and 9 months	167	Behavioral assessment	Aggression (+)
B	Sinn et al.	2010	(58)	Protection: military working dog patrol-only certification	GSD, BM, and DS	1–3 years	1,000	Behavioral assessment	Search focus (+), sharpness (+), frontal bite (+), search stamina (+), static object interest (+)

BMD, Bernese Mountain Dog; BM, Belgian Malinois; BT, Belgian Turvuren; DH, Dutch Herder; DS, Dutch Shepherd; ECS, English Cocker Spaniel; ESS, English Springer Spaniel; GR, Golden retriever; GSD, German Shepherd Dog; GWPX, Labrador-German wirehaired pointer cross; LBX, Labrador-Bernese Mountain Dog cross; LGX, Labrador-Golden retriever cross; LR, Labrador retriever; RP, Royal Poodle; RS, Russian Spaniel; SP, Saint-Pierre; V, Vizsla.

role (i.e., assistance, detection, and protection), included studies were published between January 1983 and November 2020. In the vast majority of these studies, the outcome metric used was qualification—i.e., successful placement—as an assistance, protection, and/or detection dog, with the alternative being that the dog was deemed unsuitable and released for behavioral shortcomings. For a handful of studies, the outcome measures were instead performance on specific job-related tests [e.g., on working dog trials: (94); on a Military Working Dog suitability test: (95); on an annual search test: (93)] or trainer assessment of ability (63, 82, 85, 96). And finally, two studies addressed the longer-term efficacy of working dogs and therefore only included subjects that were already initially placed as detection dogs; the first study investigated factors contributing to the longevity of a successful working dog career by comparing active dogs vs. those that had qualified but were subsequently withdrawn from service (61), while the other analyzed what behavioral features predicted speed of drug detection (92). Although not every aspect of behavior measured in each of these studies predicted success, at least a subset of measures in all of these studies had some predictive validity.

Behavioral Measurements

Across these studies, behavior was measured in two main ways. The first method, labeled in **Table 1** as behavioral assessment, refers to experimental approaches in which dogs were presented with a set of tasks, situations, and stimuli while their behavior was coded or scored by a trained rater in a standardized way. One example of this sort of assessment is the Dog Mentality Assessment (DMA), designed by the Swedish Working Dog Association, which consists of nine subtests involving social encounters, play opportunities, unexpected events, and work-related scenarios such as searching and protection [e.g., (94)]. Another example is the In-For-Training (IFT) test, often used by assistance dog schools, which exposes a dog to six potentially stressful scenarios, including a looming object, a sudden noise, and a threatening stranger, in order to gauge the dog's initial reaction and subsequent recovery [e.g., (79, 83)]. While the majority of test batteries, like the DMA and IFT test, focus on temperament traits, it is also becoming increasingly common to track the cognitive abilities of dogs, as in the Dog Cognition Test Battery [e.g., (82, 91)]. These sorts of empirical evaluations of temperament and cognition are helpful because they can be objectively scored by a small number of trained observers and the standardized format allows for direct quantitative comparison between individuals. Furthermore, in many cases, results from these tests are robust to variation in scoring methodology and are reliable whether an evaluator codes discrete behaviors or assigns an aggregate rating (46, 85, 86). However, because these assessments are often administered at just one or two timepoints, they provide a "snapshot" that may not be representative of the dog's behavior in other contexts or points in time. Furthermore, these tests can be quite labor and time intensive to administer.

The second method of measuring behavior involves ratings by puppy raisers or trainers that reflect the subjective impressions, formed over a period of weeks or months, of someone who has spent a lot of time with the dog. Rather than watching

a dog encounter different scenarios in real-time, the evaluator reflects on the dog's typical response to a variety of situations when filling out a questionnaire. An example of this approach is the Canine Behavioral Assessment & Research Questionnaire [C-BARQ; (98)], a survey that is usually completed by the puppy raisers of assistance dogs at 6 and 12 months, but can also be completed by the handlers of adult dogs. It asks the respondent about the frequency or severity of behaviors that fall into multiple categories, including aggression, fear, attachment, excitability, and trainability [e.g., (62, 79, 83, 95)]. Another example of this type of instrument is the Dog Impulsivity Assessment Scale [DIAS; (99)], an 18-item questionnaire that requires the respondent to indicate level of agreement on items about behavioral regulation, aggression, response to novelty, and overall responsiveness [e.g., (61)]. Questionnaire surveys are advantageous in that they allow for information-gathering on a large number of dogs in a short amount of time. Furthermore, each evaluator has extensive knowledge of the dog's temperament, preferences, and habits, accrued by watching the dog navigate many different real-world environments and circumstances on repeated occasions. However, having so many different evaluators can have its drawbacks as well; evaluators receive no training, what might constitute high levels of a behavior to one person might seem inconsequential to another, and evaluators may not always have sufficient contact or context to make accurate assessments. Thus, a handful of studies have benefitted by using data from both behavioral assessments and questionnaires in their predictive modeling (79, 80, 83).

Behavioral Traits Associated With Working Dog Outcomes

In reviewing these studies, some common themes emerge regarding both desirable and undesirable behavioral traits in a candidate working dog (**Figure 1A**). For example, regardless of specific career path, multiple studies supported the notion that successful working dogs are highly trainable. Trainability and responsiveness was assessed using trainer ratings (84, 86), behavioral tasks (76), and questionnaires like the CBARQ (83, 95), puppy training supervisor questionnaire [PTSQ; (77)], and DIAS (99), which include multiple items asking the respondent to evaluate the dog's propensity to follow commands, learn new tasks, play fetch, attend to relevant stimuli, ignore distracting stimuli, and respond to correction. Additionally, using a measure of trainability based on an expert observer's assessment of ease and speed of learning new tasks, Lazarowski et al. (88) found that detection dogs specializing in alerting to person-borne explosives scored significantly higher than standard explosives detection dogs. Other important traits across all working dog categories included those which facilitate a steady, positive response to the environment: successful working dogs routinely displayed confidence or an absence of fear (46, 86, 94), whereas unsuccessful dogs tended to be more anxious, and fearful of dogs, strangers, and non-social stimuli (49, 62, 76, 77, 79, 80, 83, 87, 95). The one exception to this was a study which found that Military Working Dogs who evaluators approved for further training displayed higher levels of fear-related behavior, such as barking, support-seeking, and active avoidance, than non-approved dogs (96). Finally, unsuccessful candidates were also more likely to exhibit body and touch sensitivity—i.e., uncomfortable and tense reactions when being physically handled during events like grooming or physical examinations (77, 83, 95).

The literature also identified a suite of traits associated specifically with assistance dog outcomes (i.e., that apply to both guide and service dogs; **Figure 1B**). For example, multiple studies indicated that aggression, whether evaluated by puppy raisers (83), trainers (49), or both (79), was negatively linked to success. Opportunistically chasing small animals (62) and displaying high levels of reactivity, measured across scenarios involving exposure to sudden loud noises, prey-like objects, and unfamiliar stimuli (72, 76, 80, 83), were also predictive of poor outcomes. Relatedly, dogs rated as having high levels of energy, excitability, and hyperactivity were less likely to be placed as assistance dogs (62, 73, 77). In particular, behavioral manifestations of these traits—specifically, pulling on the leash (62) and inappropriate vocalizing (78, 83)—were associated with disqualification from assistance dog programs. Taken together, these findings paint a picture of an ideal assistance dog who is relatively quiet, calm, and unobtrusive. These findings are intuitive given that, whether picking up a dropped credit card or steering their handler around a pothole, both service and guide dogs frequently work in public settings where they must exhibit socially acceptable behavior.

Whereas guide and service dog populations share certain qualities that are either coveted or problematic with respect to their success, there are other features that they do not necessarily hold in common. For guide dogs specifically (**Figure 1D**), exhibiting high levels of distraction, and especially distraction with regards to other dogs, has been repeatedly identified as a trait that is detrimental to successful placement (49, 72–74, 76, 77). Furthermore, dogs who were visibly anxious around stairs (77, 79) or in training kennels (74, 79) were also less likely to graduate as guides. Finally, one study found that guide dog candidates who performed poorly and engaged in perseverative behaviors on a multistep problem-solving task were more likely to be released from the program, providing the first evidence that variation in cognitive skills can hold valuable clues about working dog potential (78). In terms of favorable qualities, successful guides ranked high on ability to cooperate—i.e., willingness to please (71), docility—i.e., high levels of tractability and learning ability (73), courage—i.e., once frightened, the ability to overcome that fear (71), and adaptability or nerve stability—i.e., ability to concentrate in high-stress situations but remain calm in frightening scenarios (71, 77). Interestingly, strength and directionality of paw preference (believed to be a proxy for lateralization in the brain) were also linked to guide dog success (72, 75). One potential explanation for this finding is an association between motor laterality and fearfulness, which has been indicated by past studies (100–102). Taken together, studies suggest that being able to effectively focus attention and problem solve, as well as exhibiting an adaptable attitude, are key factors to guide dog success.

In terms of behavioral traits particular to service dogs (**Figure 1E**), Weiss (63) found that dogs who displayed high levels of panic behavior—operationalized as vertical activity (i.e., rearing up) when left alone in an empty room for a

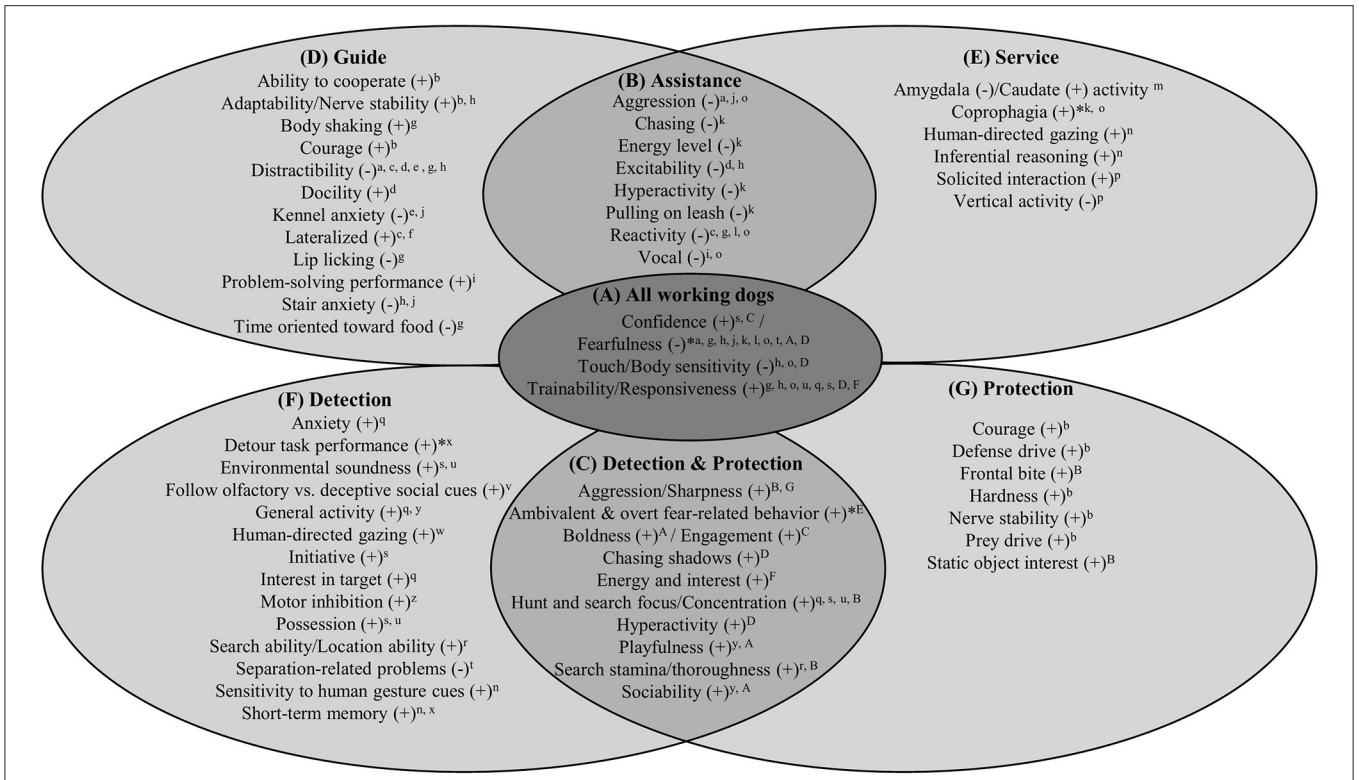

FIGURE 1 | Behavioral traits implicated in the literature as associated with working dog outcomes. Here, we list the traits that have either been positively (+) or negatively (–) linked to successful working dog outcomes, categorized in the following ways: **(A)** traits common to all working dogs within the scope of this paper, **(B)** traits common to all assistance dogs, **(C)** traits common to all detection and/or protection dogs, as well as distinct traits unique to **(D)** guide, **(E)** service, **(F)** detection, and **(G)** protection dogs. These lists of traits are based on findings from the 33 empirical studies described in **Table 1**, and we have preserved the terminology used in the original papers. The relevant papers are referenced in superscript next to each finding, using the letters assigned to each paper in the first column of **Table 1**. It is worth noting that these findings are merely a reflection of the current literature; therefore, it could be the case that some of the traits that are only listed as important for guide dogs might also be important in service dogs, but the association has yet to be explicitly tested. In rare cases, the empirical studies supported contradictory results, and in those instances the disagreements are indicated with an asterisk.

short time—were more likely to be rated as having low service dog potential. Intriguingly, Bray et al. (83) also found that coprophagic dogs were more likely to graduate as service dogs; however, Duffy and Serpell (62) found no difference in coprophagic tendencies between successful and released dogs when looking across five guide and service dog organizations. Finally, recent research has also identified cognitive abilities that appear to be useful to service dogs. Graduate dogs consistently displayed higher levels of social looking across multiple experimental contexts, including a social referencing task and an unsolvable task (82). Given that service dogs must respond to human-given commands, these results are consistent with the type of behavior that is expected from a service dog in performing their day-to-day duties. Furthermore, using awake fMRI, Berns et al. (81) determined that certain brain activity patterns observed while the dog was viewing trained hand signals, including increased caudate activity and decreased amygdala activity, predicted success in a service dog program. Thus, for service dogs, a calm temperament and a strong propensity to direct attention toward humans appear to be beneficial.

In evaluating studies of dogs who engage in protection and/or detection work, a set of different (and sometimes opposite) characteristics materialized as important when compared to assistance dogs (**Figure 1C**). First, these dogs embodied a much more active phenotype: successful dogs scored higher on C-BARQ items indicating that they were hyperactive and had difficulties settling down, as well as prone to chasing shadows or light spots (95). Additionally, active military dogs and police dogs from multiple countries routinely showed high levels of energy and interest in their surroundings (61), as evaluated through the Positive and Negative Affect Scale (103). Successful military working dogs were also more bold, meaning they were sociable toward a stranger, playful during tug-of-war, chase-prone when presented with a moving object, and curious about startling events (94). They were also generally more willing to engage with their social and physical environment (46). Playfulness and sociability were also found to be associated with quicker drug detection times in a population of detection dogs, but only for German Shepherd dogs (92). Furthermore, unlike in assistance dogs, aggression was a desirable trait for detection and protection

jobs; dogs who exhibited aggression and "sharpness"—i.e., a willingness to respond aggressively—in early adolescence were more likely to become police (97) or dual-certified military working (58) dogs. Unsurprisingly, successful protection and/or detection dogs also had a propensity to excel with search-related skills (85, 86, 88). For example, a high score on search focus—i.e., the ability for sustained, independent, olfaction-driven investigation without fatigue—was associated with both patrol-only and dual-certified qualifications (58). Overall, exemplary protection and detection working dogs appear to be energetic and assertive, and exhibit focused and thorough searching.

As a group, detection dogs also exhibited specific temperamental and cognitive phenotypes, as well as functional abilities related to their job (**Figure 1F**). High levels of activity, whether measured through a behavioral test (92) or trainer ratings (84), were linked to positive outcomes in drug detection dogs. In contrast to guide dogs, heightened anxiety was also indicated to be beneficial to drug detection dogs (84). Anxiety loaded together with other traits, including general activity, onto a component labeled "desire for work" that was associated with qualification (84). However, in search-and-rescue dogs in particular, separation-related anxiety was a negative trait; lower instances of separation-related problems were associated with FEMA-certification (87). Finally, multiple studies linked successful outcomes to the dogs ability to comfortably and adaptively respond to their physical and social environment, referred to as environmental soundness (86, 88) or initiative (86). In terms of cognitive skills, several studies provide evidence of the importance of social cognition. When presented with an unsolvable task at 11 months of age, dogs who eventually went on to qualify as detection dogs spent more time gazing toward the human (90). Furthermore, the ability to follow a human communicative gesture in a cooperative food-finding context was also linked to explosive detection dog success (82). Crucially, however, when olfactory and social cues were pitted against one another, the tendency to make choices guided by olfactory cues over misleading social cues predicted detection dog success (89). Cognitive skills outside the social realm were also significant; positive detection outcomes were linked to increased short-term memory (82, 91), better motor inhibition (93), more correct choices during the acquisition phase of a detour task, and longer latencies to detour during the first reversal trial of that same detour task (91). There were also several job-specific behaviors that differentiated detection dogs who qualified from those who did not. Successful detection dogs were extremely interested in an object doused in scent (84), possessive of objects (86, 88), and quick to locate hidden explosives without assistance from the handler (85).

Finally, the literature identifies several traits which appear to be advantageous in protection dogs (**Figure 1G**). Similar to guide dogs, successful protection dogs exhibited high levels of courage and nerve stability, meaning that they reacted appropriately and were resilient and focused when faced with high-stress or frightening scenarios (71). Additionally, effective police dogs showed high levels of "hardness," indicating that neither corrections nor frightening experiences affected them strongly (71). They also displayed other traits which are related specifically to the function of protection dogs. For example, patrol certification was more likely for dogs who exhibited a strong frontal bite and extreme interest in a rubber toy (58). Relatedly, police dogs showed an especially high drive to engage in competitive games—i.e,. prey drive—and a tendency to defend themselves and their handlers—i.e., defense drive (71).

Although the studies reviewed here are highly informative about relevant adolescent and adult behavior, it is widely acknowledged that the earlier an accurate prediction can be made about the ultimate suitability of a potential working dog, the better. Thus, there is longstanding interest in aptitude testing with puppies. However, evidence regarding whether adult characteristics can be accurately predicted from those of puppies remains mixed. While there are several studies that find evidence for long-term stability in temperament (76, 77, 104–109), others find little evidence for these associations (110, 111). Furthermore, while cognitive traits have been much less studied, there is emerging evidence that some traits, such as those related to executive function, social communicative skills, and odor discrimination, show moderate stability over time, while others, such as memory and auditory discrimination, do not (91, 112). Finally, while multiple studies have found that early screening (i.e., 12 weeks or younger) of puppy temperament is not very effective in predicting working dog success (104, 113, 114), there are others that suggest assessments of puppy behavior do have some predictive value (97, 106, 107). Given their potential utility, and the fact that we continue to refine our understanding of which traits are most important, more research into the predictive value of puppy testing is clearly warranted.

The studies reviewed above identify aspects of behavior and cognition that are associated with working dog success; however, the causes of variation in these traits remain poorly understood. Given the complex nature of most behavioral and cognitive processes, we expect that these traits will be influenced by both environmental and genetic factors. Although knowledge about these processes remains limited, we review key findings about environmental and genetic associations with working dog success in the following two sections.

Environmental Factors

Early environmental experiences are known to have profound and lifelong effects in many animals. For example, in rodents and primates, the amount and type of maternal care experienced by infants has wide-ranging effects on later development. Extreme disruptions in early maternal care (e.g., 1–3 h separation over multiple days, or a single 24-h separation period) adversely impact later offspring cognition (115–117), whereas shorter separations from the mother and social group appear to have inoculating effects, dampening stress responses (118) and enhancing cognition (119, 120). Importantly, even natural variation in the quantity and quality of maternal care that offspring experience over early development has been demonstrated to have long-lasting effects on later stress responses (121), behavior (122, 123), and cognition (124, 125).

Recently, it has been suggested that the same is true in dogs, with maternal care posited to play a crucial role in the behavioral development of puppies (126–128). As we learn more about

the optimal maternal conditions for working dogs (see section 1.2.1 below), people who procure dogs should consider the early environmental conditions that candidate dogs experienced. While more research is needed, it seems clear that an objective measure of maternal care could be one useful future metric when predicting a dog's working potential (78).

It is also likely that experiences during the juvenile period, lasting from ∼12 weeks to 6 months, are similarly formative. Unfortunately, canine research covering this time period is scarce (129). However, the few studies that have been conducted in working dogs provide support for the notion that the environment over this period has important impacts on behavior in adulthood (130). For example, Serpell and Duffy (131) surveyed the puppy raisers of over 975 prospective guide dogs about their dog's behavior as well as features of the dog's environment. They found significant effects of many aspects of the home rearing environment on dog behavior measured at 12 months of age. Living with a more experienced puppy raiser (quantified as number of trainee guide dogs previously raised) was associated with less aggression toward people and dogs, as well as lower levels of dog-directed fear, non-social fear, and touch sensitivity. Being raised in a household with other dogs was also associated with less aggression toward household members. Finally, reported traumatic events during the juvenile period had significant effects on later expression of defensive behaviors, with dogs who were attacked or threatened by an unfamiliar dog exhibiting higher levels of dog-directed fear and stranger-directed aggression, and dogs who were frightened by a person exhibiting high levels of stranger-directed fear. In a similar study of a different guide dog population, Harvey et al. (132) also found effects of puppy raiser experience and the social environment. Puppy raiser experience was associated with lower levels of energy and distractibility. In terms of the social environment, being raised in a household with other dogs and children was associated with higher energy levels, excitability, and trainability. Additionally, dogs who were given more opportunities to play with other dogs scored lower on separation-related behaviors. Importantly, many of these behaviors are in turn associated with working dog outcomes.

And in fact, two studies have linked certain aspects of juvenile dogs' experiences directly to working dog outcomes. Foyer et al. (95) found that trainee military working dogs who were left home alone for longer periods during the day were subsequently more successful. The authors note that, as this finding was correlational, it is likely the case that being left alone longer was more feasible in dogs who were more resistant to stress, a behavioral feature that is desirable in working dogs. Regardless of the mechanism, it reveals an easily monitored feature of the early environment that can be a useful indicator for future working dog outcomes. In guide dogs, Serpell and Duffy (131) found that experiencing a traumatic event—specifically, being frightened by a person—was significantly associated with a lower likelihood of becoming a guide, whereas being raised in a household with other dogs and pets was significantly associated with a higher likelihood of becoming a guide. Again, these are fairly straightforward measures that can easily be reported by the puppy raiser.

Genetic Factors

Although there remains much to be learned about the genetic bases of complex traits in dogs, it is already clear that many behavioral traits critical to working dog success are strongly influenced by genetic factors (114, 133–136). As described below (see section 1.2.2), this knowledge has important applications in the context of breeding dogs for working roles. However, genetic factors can also be considered when attempting to identify dogs with potential for success. Here, it is important to distinguish between approaches based in quantitative and molecular genetics (137). Quantitative genetic approaches make use of knowledge regarding the heritability of particular traits, and relatedness between individuals in a population. Estimated breeding values (EBVs) reflect an animal's genetic merit with respect to a phenotype of interest and incorporate the heritability of this trait. When candidate dogs are selected from a population in which phenotypes, relatedness, and heritability of key traits are known, EBVs provide a useful measure for identifying dogs with the most genetic potential for success. Using molecular genetics, it is also possible to estimate an animal's phenotypic potential using marker-assisted selection. As the name implies, this process relies on screening animals based on known genetic markers that are associated with the phenotype of interest. This method has advantages in that an animal's potential can be estimated directly from their genotype, and this approach has flourished in plant and production animal breeding (138). Although marker-assisted selection and successor approaches such as genomic selection—which makes use of variants throughout the genome—are expected to become increasingly common, at present they entail notable challenges in terms of implementation with dogs [(139), Karlsson et al., submitted this volume].

Nonetheless, early work has identified some genotypic markers that may be useful in the selection of working dogs. In general, domestic dogs have been found to be hyper-social compared to non-domesticated canids, which is one factor that likely facilitates their success living and working in human environments (140). Structural variants in *GTF2I* and *GTF2IRD1* genes have been linked to extreme sociability in dogs in general (140). However, individual variability between dogs also exists. Hyper-focus to social stimuli and heightened gregariousness is often considered desirable for some working roles, such as therapy and assistance dogs. On the other hand, it may also interfere with a dog's ability to cope when left alone or to focus on non-social stimuli, skills that are critical to independent problem-solving success central to other working roles (141). Therefore, in some cases genetic screening may provide an opportunity to match dogs with training or working opportunities that capitalize on their behavioral predispositions, and help them achieve their full potential. However, it is important to note that even in dogs predisposed to high sensitivity to social stimuli, best practices in socialization and training are still critical to the quality and success of social interactions with humans, in addition to the dog's well-being.

For detection and protection dogs, more preliminary molecular genetic approaches have been undertaken. For example, a variable number tandem repeat (VNTR) in a

neurotransmitter-associated gene, Tyrosine Hydroxylase (*TH*), has been associated with impulsivity in dogs (142) and even the probability of success in a Korean military dog training program (143). Further, targeted candidate gene approaches have had preliminary success in identifying dogs with the greatest potential in Korean military dog programs (144, 145). Additionally, a candidate gene approach recently identified several single nucleotide polymorphisms (SNPs) associated with variable canine olfactory detection performance (146, 147), suggesting that a molecular genetics approach may be fruitful in identifying detection dogs with higher performance capabilities. However, more research and application to other populations of working dogs is necessary before robust conclusions can be drawn or such a technology can be implemented as a selection tool.

Dogs Who Choose Their Own Jobs: Accounting for the Preferences and Skill Set of the Dog

Most programs that raise and train working dogs are focused on a single career path, whether that is assistance or detection work. As a result, the success rate of the dogs in these programs is often limited [e.g., 50% or less; (62)]. An alternative approach is to identify the essential foundational skills that are required by all working dogs and then select for the dogs with those skills combined with general health characteristics. Then, the dogs can be exposed to basic training before undergoing reproducible and valid screening tests to determine their physical and behavioral strengths and preferences. For example, a future search-and-rescue dog needs to be comfortable working independently of the handler and moving confidently over unstable surfaces. If a dog does not have these natural tendencies, with training and a lot of effort, they may be able to achieve the basic skills to function as a search-and-rescue dog, but a dog that has natural tendencies for these skills will reduce the necessary training time and increase the likelihood of success. Additionally, from a welfare perspective, expressing natural behaviors is thought to be intrinsically rewarding to a dog (148). In order to maximize the success of working dogs and thoughtfully place each dog in a role that is suited to that dog's physical abilities and temperament, the phenotype associated with each career path needs to be clearly defined and tests validated to predict performance. This approach is analogous to the screening measures described above, but rather than initially screening for specific cognitive or behavioral characteristics, it instead allows dogs to first engage in basic components of a variety of working roles, providing important insights about natural proclivities for various components of these jobs.

Improving and Cultivating Characteristics Linked to Working Dog Success

The studies reviewed above address methods for potentially identifying dogs with high potential for success, which can be considered as a type of "aptitude testing." However, a complementary approach involves active intervention to cultivate desirable phenotypes. This process can be effectively implemented at two distinct levels. First, at the individual level, we can intervene over the course of dogs' lives to set them up for success in several ways, including manipulating their early environment, promoting healthy habits, and intentionally fostering desirable qualities. For maximum efficacy, these approaches require early access to the dogs who will ultimately be trained for working roles. Second, at the population level, we can intervene over generations to strengthen future populations of dogs through genetic selection of heritable traits. This second approach will be most feasible for programs that breed their own dogs or function as part of a breeding cooperative, as it requires access to pedigrees and the ability to estimate heritability of various traits within a particular population.

It is worth noting that intervention at both the individual and population level necessitates a clear understanding of which traits are desirable for each of the career options. Below, we review the best practices as suggested by the literature. However, as our understanding of which characteristics contribute to working dog success continues to grow and evolve, that will directly inform the environmental features, physical characteristics, and behavioral traits that should be targeted for improvement. Furthermore, some suggestions will apply to characteristics that benefit all working dogs—for example, all working dogs need healthy hips, whether they are an assistance dog or a detection dog—whereas others will be specific to certain roles; for example, the ability to effectively use olfaction is crucial for a detection dog but largely irrelevant for most assistance dogs.

Modifications at the Individual Level: Evidence-Based Improvements in Rearing and Training Practices

Early Environment

In recent years, several studies have reported associations between early maternal environment and later offspring behavior. For example, after surveying the families of over 3,000 Finnish dogs, Tiira and Lohi (149) found, based on owner-reported measures, that dogs who experienced lower levels of maternal care displayed higher levels of fearfulness as adults. In an observational study in which Beagle dogs whelped in a professional center, researchers coded maternal behavior and found that puppies who experienced higher levels of maternal care over the first 3 weeks of life were more exploratory and showed lower levels of anxious behaviors, such as vocalizations and increased movement, during a 3-min isolation task administered at 2 months of age (150). Interestingly, a second study by the same group observed pet dogs of various breeds who whelped in family homes and found essentially the opposite result, wherein higher levels of maternal care were associated with more stress behaviors and less exploration and play in the eight-week-old puppies (151). These differences raise interesting questions about how the expression of maternal care potentially differs between populations of dogs, as well as how maternal care interacts with other aspects of the early environment to affect offspring characteristics.

While these studies were not conducted in working dogs, the behaviors found to be associated with maternal care have substantial overlap with those perceived as important to working dog roles. Furthermore, in a study that did specifically examine military working dogs, Foyer et al. (152) found an association between maternal behavior and later puppy behavior over 1

year later—-German Shepherd dogs with more involved mothers were more interested in people, more comfortable in novel environments (e.g., on metal stairs or shakey tables), and more aggressive. Bray et al. (78) conducted a study in a population of guide dogs and found that high levels of maternal behavior were linked to stress and anxiety in the offspring as adolescents (i.e., higher activity levels in an isolation task and a reduced latency to vocalize during a novel object task), as well as worse performance on a problem-solving task. This same study also directly linked maternal style, experienced by the puppies over the first few weeks of life, to working dog outcomes as adults. Puppies whose mothers displayed higher levels of maternal care, operationalized as nursing, licking/grooming, contact, and proximity (153), were less likely to succeed as guide dogs up to 2 years later. Furthermore, puppies whose mothers more often nursed from a sitting or standing position were more likely to graduate as guide dogs. One potential explanation for these findings is that small doses of mild stressors—i.e., having an adequate but less responsive mother, nursing from a more challenging position—might help to facilitate resilience from a young age. This idea of mild stressors leading to positive long-term outcomes is echoed in the handling literature, wherein introducing brief separations from the mother and handling (i.e., tactile stimulation) by a human in the first few weeks of life has been associated with positive emotional and cognitive outcomes in both rodents (154–157) and dog puppies (158–160). Thus, especially as we continue to learn more about the long-ranging effects of early environment over the first few weeks in dogs, breeders can use these findings to encourage and generate optimal conditions.

Additionally, the timing and circumstances under which puppies are introduced and acclimated to social stimuli, such as people, along with a diverse sampling of environmental features, are critical. For example, it is well-established that experiences during the socialization period, which encompasses the time window from roughly 2.5 to 14 weeks (129), can have major implications for later behavior (161). In working dogs specifically, guide dog puppies that were whelped in a kennel and first integrated into a home environment at 12 weeks of age were significantly more likely to later graduate as guides than puppies who did not leave the kennels until 13 weeks of age or later (162). However, the ideal weaning time, especially as it pertains to working dogs, is both understudied and debated in the literature (129). On the one hand, 6–8 weeks has been identified as the best time to start building the human-canine bond and begin gaining exposure to aspects of the later working environment (163, 164), and yet there is also evidence that weaning too early can be overly stressful, adversely affecting health and behavior (165–167).

As puppies develop, proper socialization through exposure to varied stimuli, ideally prior to 14 weeks of age, is key to the dog becoming a well-adjusted and resilient adult (54). Early, consistent experience with speech and music via radio clips (168) and video images (169) during the first few weeks of life have been linked to decreased noise reactivity and neophobia, respectively, around 7–8 weeks of age. Relatedly, a lack of exposure to urban environments between 3 and 6 months of age was associated with aggressive and avoidant behaviors (170). There is also evidence in military working dogs that increasing their amount of human contact—i.e., housing dogs with their handler instead of kenneling, implementing a socialization program—is associated with decreased fear and aggression (171, 172). However, while experts agree that exposing puppies to all of the environmental features that they will encounter over the course of their job is essential, this exposure should be done in an intentional, controlled way. For example, when first introducing dogs to specific fear-eliciting stimuli, optimal responses were obtained when dogs were first given the chance to habituate (173). Furthermore, the social context during exposure to novel and/or potentially scary stimuli is important to consider; when a dog is given the opportunity to observe how conspecifics and/or humans react to a given situation, it can in turn inform how the dog reacts, either positively or negatively (54, 174).

Physical Soundness

Physical soundness is based on the structure and physical conditioning of the dog. Much of the structure will be a function of genetics. Dogs with physical limitations such as heart conditions, respiratory compromise from brachycephalic syndrome, and/or musculoskeletal or sensory anomalies are unlikely to be effective working dogs. Physical conditioning provides an opportunity to enhance the dog's health, behavior, and longevity. However, implementation of a formal exercise program for puppies has been subject to controversy, and there is currently little data to support definitive recommendations. Most of what is known about exercise during development is derived from animal research studies or human reports (175–177). The primary concern about early introduction of exercise is related to the potential effect of repetitive motion on bone growth and joint development. One observational study of puppies $<$ 3 months of age reported an increase in hip dysplasia in puppies with access to stairs (176, 178), although the same study reported a decreased risk in puppies with access to off-leash exercise. In an intensive treadmill study of young Beagles, the bones and joints of the limbs were not adversely affected; however, early evidence of osteoarthritis was detected in the spine (179). Most studies find there are benefits to moderate exercise during development, including mental stimulation, improved muscle development, joint stability, bone development, and coordination. Physical activity and the associated increase in muscle strength and joint stability as well as decreased body fat leads to a decrease in the development of osteoarthritis (180, 181). Continuation of an exercise program throughout the life of the dog is likely to decrease injury and improve recovery from injury. A recent foundational fitness program for working dogs has been proposed for working dog puppies through adults (182). This Fit to Work program focuses on mobility, stability, strength, and proprioception and avoids repetitive high impact activities. As a foundational program, it does not address job-specific physical requirements or cardiovascular stamina, which should be tailored for individual careers. Finally, in addition to the physical benefits, daily exercise is linked to a decrease in both noise sensitivity and separation anxiety (149), as well as improved quality of life scores (183). Regardless of the age of the dog or the career path, some component of physical exercise is essential for the physical and behavioral health of working dogs.

Behavior (Temperament and Cognition)

To foster desirable behavior, one technique which organizations could implement is to work with puppy raisers to more systematically track cognitive and temperamental tendencies of interest in each dog from an early age, and to then provide tailored advice and support (184). By doing so, potential red flags could be identified earlier and then actively addressed during rearing and training. Additionally, decisions could be made earlier about which working dog path might be the right fit. One way of achieving this goal is through prescriptive (as opposed to predictive) testing. An example of this sort of practical diagnostic tool that has recently been developed for pet dogs is the AKC Temperament Test [ATT; (185)], which evaluates a dog on a set of standardized tasks that allow problem behaviors to be identified. As part of the testing, concrete training materials are then provided in order to help the raiser modify any problematic behaviors. In fact, evidence-based training techniques are likely to be instrumental in influencing the behavior and subsequent success of working dogs, during the puppy raising phase but especially during the professional training phase. For a detailed discussion of best practices in working dog training, please see Hall et al. (submitted, this volume).

In some cases, dogs may work part-time and live as pets with their owner or handler when not working—for example, this is true for many volunteer search-and-rescue dogs (42) as well as therapy dogs (186). It is also true that not all dogs who serve in a working role were specifically bred or selected for that purpose initially. For example, a dog may become an assistance animal for their owner, or another individual in the home, after living primarily as a pet in that same household previously. Even in cases where dogs were bred specifically for a working role (i.e., an individual bred and raised to be a guide dog), the connection shared between the dog-human pair often extends beyond that of a working relationship. In all of these cases, considering the quality of the dog-human bond may be an important and relevant factor for predicting the dog's work performance, as well as the well-being of both the dog and human involved. A growing area of research is focused on attachment bonds developed between dogs and humans (187–189) and is relevant given that attachment security is broadly associated with stress reduction, resilience, comfort in novel situations and environments, and exploration and learning in both humans and dogs (190, 191). There is considerable research demonstrating that how a human perceives the quality of the relationship they share with a dog—for example, how attached they are to the dog they own—can have a significant impact on human health and well-being (189, 192). Several studies have also documented the benefits (e.g., increased well-being and job satisfaction) of a close relationship to the dog with whom the handler works across animal assisted therapy (192), assistance dog (193), and protection/detection dog (43) contexts.

Less research has focused on the impact of a dog's attachment security toward their owner/handler on their own well-being and performance. However, the research that has been done has suggested that working dogs with a secure attachment to their handlers exhibit more resilience and faster stress reduction in novel environments (191, 194, 195), may perform better in therapeutic contexts (191, 196), and are more persistent at problem solving (190) when compared to dogs with insecure attachment bonds. Dogs are also known to form attachment bonds to new humans rapidly (197, 198), even into adulthood (199). Furthermore, research suggests other, related aspects of working dog-handler relationships are associated with overall performance; avalanche search dogs who were confident working farther from their handler were more successful (200), and detection dogs with higher levels of familiarity with their handlers were more effective (172, 201, 202), as well as less fearful and aggressive (171). When surveyed, Transportation Security Administration (TSA) detection dog handlers reported that they viewed the relationship to the handler as one of the most important traits for work; however, it is not currently accounted for in the organization's behavioral tests (70). A more thorough investigation of how relationship quality between dogs and their owners, handlers, trainers, and other humans they encounter in their working role impacts performance and welfare is an important area for additional future research. However, the current research suggests that taking the time to foster a strong bond and familiarity with the dog's working partner is one avenue through which to improve working dog performance.

By facilitating healthy, happy, and resilient puppies from the first few weeks and continuing across development, the hope is that these dogs will be better prepared to face the cognitive and temperament challenges awaiting them on the job, ultimately resulting in lower attrition rates from working dog programs.

Modifications at the Population Level: Breeding for Working Roles

The practice of breeding for particular characteristics in dogs has ancient origins and is responsible for the extraordinary phenotypic variation among modern breeds (134, 140, 203, 204). Because many working dog organizations maintain (and share) dedicated breeding populations, there is great potential for continual improvements in these populations through selective breeding. However, it is important to note that the effectiveness of this approach relies on both an understanding of the genetic and environmental influences on particular traits, as well as reproducible methods for measuring phenotypes of interest (139). Heritability—i.e., the proportion of variance in a trait that is due to additive genetic factors—is a key determinant of the potential for selective breeding. Highly heritable traits respond strongly to selection, thereby providing opportunities for rapid improvements in a population. In contrast, traits with minimal heritability present less attractive targets for breeding, and in the case of traits with no heritability, selective breeding is futile. Below, we highlight several opportunities and areas of progress in the breeding of better working dogs.

Physical Soundness

With respect to physical health, appropriate health screening of working dogs is critical prior to selecting breeding pairs or working dog candidates. A complete medical evaluation includes an eye examination, cardiac auscultation, and ultrasound if indicated. Genetic diseases known to affect the breeds being used (e.g., degenerative myelopathy in German Shepherd dogs,

exercise-induced collapse in Labrador retrievers) should be cleared by heritage or by testing. Mobility is required for all dogs and essential for working dogs. One of the most common causes of early retirement in military working dogs is spinal cord disease and arthritis (60, 180, 182, 205).

Although phenotypic screening can be important in breeding decisions, phenotypes of individual animals arise through a combination of genetic and environmental factors. More direct approaches to identifying genetic merit use estimated breeding values (EBVs), which can be informed not only by the characteristics of an individual dog, but also by their relatives, and knowledge of the heritability of the trait(s) in question, while adjusting for environmental effects. The use of EBVs, which is widespread in production animals (206), has become more common in dog populations in recent decades (207). For EBVs to be most effective, it is crucial to have values on phenotypes of interest from as many members of the population as possible (i.e., not just the potential breeding dogs, but also their siblings, parents, and grandparents). These measures have been used successfully for genetic improvements in hip and elbow dysplasia, which are conditions that lead to secondary osteoarthritis, compromise dog welfare, and can shorten the livelihoods of working dogs. Due to the relatively high heritability of these traits (47), some working dog organizations have drastically reduced their incidence through selective breeding programs. For example, in a study across three different breeds, the percentage of dogs with "excellent" hip scores was increased from 34–55% to 87–94% within eight generations of selection (208).

Behavior (Temperament and Cognition)

Breeding for behavioral traits has proven to be more difficult, in part due to the challenges of large-scale adoption of standardized phenotyping procedures. Currently the genetic contribution to many behavioral traits remains poorly understood, but heritability studies are becoming increasingly common (71, 133, 134, 136, 209–214). To our knowledge, most working dog organizations that currently incorporate behavioral measures in EBVs rely on organization-specific phenotyping procedures which are often tailored to specific working roles. Thus, unlike measures of disease susceptibility, which rely on highly standardized phenotypes with common value across working roles, behavior presents somewhat of a "moving target" which may be quantified and valued differently across organizations and working roles. Indeed, many of the most pressing challenges with respect to behavior involve simply identifying behaviors that predict working dog success. Only after these traits have been identified, and a heritable basis for them determined, can selective breeding move forward productively. Nonetheless, the potential to successfully select for behavioral traits conducive to working roles is suggested by the substantially higher probability of success for dogs from working dog breeding programs as opposed to outside stock of the same breeds (49, 59).

FUTURE STEPS

The work reviewed above presents promising advances with respect to both our scientific understanding of working dogs, and the practices through which these dogs are selected, bred, and trained. In fact, many of the best practices discussed will also be relevant to other types of working dogs not explicitly discussed in this paper, as well as companion dogs. For example, being intentional about selection of breeding dogs, health and genetic screening, socialization, and cultivating the human-dog bond is crucial for producing healthy, well-adjusted dogs in general. However, specifically with regards to working dogs, we recognize important knowledge gaps and limitations that will be important to overcome in the future. Thus, we conclude by identifying key limitations of current research and practice and provide recommendations for future work in these areas.

Defining and Understanding Working Dog Success and Failure

One key challenge relates to defining success as a working dog. In most studies, success has been defined primarily as completion of the associated training program and placement into a working role. While indeed a functionally relevant outcome, this measure is subject to several important limitations. First, organizations vary widely in the proportion of dogs who complete training programs and this variability arises in part due to differences in procedures, standards, and criteria across organizations. Large established organizations, who breed and train thousands of dogs per year, can afford to release dogs from training programs more so than smaller organizations who have access to limited numbers of dogs. Similarly, large organizations may be better positioned to simply release a dog from the program if this dog exhibits undesirable characteristics, rather than investing substantial effort toward trying to modify the dog's characteristics. Second, the extent to which various undesirable characteristics (e.g., minor medical problems, nuisance behaviors) are acceptable in a placement likely varies widely between programs as well. Thus, it is typically not meaningful to compare success rates between different organizations, and training success does not reflect any single set of objective criteria. Decisions to release a dog from a training program are typically made on a case-by-case basis, relying on the intuitions and judgements of training staff (rather than objective performance on a standardized evaluation). Although these decisions are made by subject-matter experts, they inherently involve a degree of subjectivity. To our knowledge, it is also rare that working dog organizations assess interrater agreement in these contexts, making it unclear to what extent independent evaluators would arrive at similar conclusions. Lastly, evaluating success based simply on completion of a training program fails to consider the extent to which a dog is ultimately able to carry out their duties once placed in the working environment.

From a practical perspective, key measures of a working dog's impact relate to the dog's ability to perform their role once placed in the working environment, as well as the longevity of successful performance in this context. Batt et al. (45) propose an important distinction between training success and working success. For example, in one large-scale study, nearly a fifth of guide dogs were withdrawn from their working roles due to behavioral problems (215), despite having successfully completed

the initial training program. However, the causes of failure in these types of circumstances can be challenging to identify. Many working dogs function as a team together with a human handler, and these handlers may vary in their skill or compliance with activities required for the dog to function effectively. Thus, the ultimate success or failure of a dog often depends considerably on the handler(s) with whom they work. Nonetheless, it is important to recognize that robust definitions of success should incorporate measures of a dog's performance in the actual working role, not merely the prerequisite training. Ideally, working dogs should undergo regular evaluations in which they are assessed or recertified by a professional evaluator to ensure they remain fit for their roles.

Tolstoy famously began his novel Anna Karenina with the phrase that "all happy families are all alike; each unhappy family is unhappy in its own way" (216). Somewhat analogously, within working dog programs, successful dogs tend to share many of the same characteristics required for success, whereas the reasons for failure are myriad and complex. Although it is convenient in research to classify outcomes as success vs. failure, it is important to recognize that the latter category will almost always consist of dogs who were unsuccessful for different reasons. In most studies to date, common problem behaviors (e.g., excessive barking, separation anxiety, dog-directed aggression) have clear negative impacts on a dog's potential success. However, each of these behaviors may have a different and complex etiology making it challenging to identify unifying themes that are shared among unsuccessful dogs. Additionally, although the presence of these types of behaviors is decidedly negative, the mere lack of problem behaviors is typically not sufficient for success. This phenomenon is nicely illustrated through predictive modeling studies in which dogs with a history of problematic behaviors can be reliably identified as having a low probability of success, whereas the lack of these behavior problems does not necessarily translate to a high probability of success (83). Thus, it will be important to understand working dog potential both in terms of the absence of problematic tendencies as well as the presence of other favorable traits required for a specific working role (130). At present, researchers have been more successful in developing assessments of the former, making tools to achieve the latter an important priority for future work.

Based on the challenges reviewed above, both dog providers and researchers should strive to develop and implement outcome measures that go beyond simple definitions of success or failure, and instead quantify dogs' ultimate strengths and weaknesses across multiple functional domains. Ultimately, these outcome measures will provide important endpoints for selection tools that not only identify a dog's probability of success, but also identify the specific areas in which a dog is likely to excel or struggle. In turn, these approaches will inform interventional strategies that can be catered to the characteristics of individual dogs.

Research Methods

Whereas studies of medical conditions and physical characteristics of working dogs have aligned on widely-used standardized assessments [e.g., hip scores; (217)], studies of working dog behavior and cognition tend to employ a greater diversity of methods. By far the most standardized behavioral measures involve survey-based assessments [e.g., CBARQ; (98)], which are relatively easy to administer identically across different populations and study designs. In contrast, experimental studies of working dog behavior and cognition are still in a period of active method development and validation, and there are few standardized research methods that have been adopted across the industry.

Although a lack of standardization can be viewed as a weakness, we argue that standardization for the mere sake of standardization does little to advance the field. Before aligning on standardized approaches, it is critical that the approaches being adopted are rigorously evaluated in terms of their validity and applicability to diverse populations and working roles. Currently many of the approaches described in this paper are in nascent phases of development and it will be important to allow them time to reach maturity before encouraging widespread adoption. During this time, communication between researchers and professionals in the field with years of hands-on working dog experience should be prioritized (64, 67, 70, 218). These conversations will help address the disconnect of researchers conducting tests that are then either not useful or not routinely used, as well as organizations running tests that have not been analyzed or validated. Crucially, as the field moves through this period of development, it is more important than ever that researchers employ rigorous experimental designs along with objective and transparent approaches to scoring and analysis, such that the products of this research can be adequately evaluated by both scientists and practitioners in the field (65). Along these lines, researchers should aim to [1] present methodological details such that all components of a study are fully reproducible, [2] conduct and report inter-rater reliability for measures used, [3] conduct and report retest reliability, [4] differentiate between approaches that describe statistical association vs. predictive validity, [5] employ well-powered designs that control for confounding factors, and [6] ensure adequate blinding between research staff and dog training professionals.

Lastly, it is important to emphasize that while we identify a range of opportunities for improving the performance of working dogs, due to diversity in working dog roles and the organizations in this arena, there are few one-size-fits-all solutions. Large established organizations who breed hundreds of dogs per year are undoubtedly in better positions to make use of selective breeding, EBVs, and potentially even genomic selection methods to improve their populations over time. Smaller organizations, and those who source dogs from more heterogeneous populations, stand to achieve larger gains through enhanced techniques for identifying individual dogs with high potential, as well as individualized interventions that would be challenging to implement at larger scales.

Although specific applications will vary across the industry, it is important to recognize that when considered collectively, the science of working dogs has enjoyed many notable advances throughout recent decades. We expect that continued

collaboration between scientists and practitioners will play a critical role in the future of this enterprise, which has great potential for enhancing the health and well-being of both working dogs and the people they serve.

AUTHOR CONTRIBUTIONS

EB, NH, EM, CO, and MU contributed to writing—original draft. EB contributed to supervision and visualization (**Figure 1** and **Table 1**). All authors contributed to conceptualization, investigation, funding acquisition, and writing—review & editing.

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Healthy, Active Aging for People and Dogs

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Dogs act as companions who provide us with emotional and physical support. Their shorter lifespans compel us to learn about the challenges and gifts of caring for older individuals. Our companion dogs can be exemplars of healthy or unhealthy aging, and sentinels of environmental factors that might increase or decrease our own healthy lifespan. In recent years, the field of aging has emphasized not just lifespan, but healthspan—the period of healthy, active lifespan. This focus on healthy, active aging is reflected in the World Health Organization's current focus on healthy aging for the next decade and the 2016 Healthy Aging in Action initiative in the US. This paper explores the current research into aging in both people and companion dogs, and in particular, how the relationship between older adults and dogs impacts healthy, active aging for both parties. The human-dog relationship faces many challenges as dogs, and people, age. We discuss potential solutions to these challenges, including suggestions for ways to continue contact with dogs if dog ownership is no longer possible for an older person. Future research directions are outlined in order to encourage the building of a stronger evidence base for the role of dogs in the lives of older adults.

Keywords: aging, dogs, human-animal interaction, healthspan, healthy aging

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INTRODUCTION

Humans and our non-human animal companions share many attributes, and perhaps none more so than the experience of aging. As we and our pets grow older, we experience a steady physiological decline, leading to age-specific increases in the risks of morbidity and mortality. Even in our youth, we observe this in our grandparents and parents, and often quite dramatically in our pets, and eventually, in our own lives.

Aging is a powerful phenomenon. In human populations, age is the single greatest risk factor for most of the common causes of mortality (1), often by orders of magnitude compared to the next most important risk factors, and aging also has tremendous psychological, social and economic impacts (2). We can think of aging as a broad, unifying principle—a conceptual bridge linking diverse ways in which we understand the world, from molecular and evolutionary biology, to demography and economics, to history and the fine arts, and more. It also provides a unique link between our pets and ourselves. Given the rapidity with which our pets age relative to us, they are a powerful reminder of what lies ahead for us, and they provide us with an opportunity to learn how to age well.

The past 30 years of aging research has led to tremendous advances in our understanding of the basic biology of aging, helping us to better understand aging both in our own species and our companion dogs. In this review we start with a brief discussion on the impact of aging in human

populations (about which we know a great deal), about aging in dogs (about which we know much less), and the similarities and differences between the two. We then turn to an exploration of how the human experience of aging impacts our relationship with dogs, and how, in turn, aging in dogs affects human-animal interaction. Finally, we consider some of the important questions that arise from a consideration of the mutual experience of aging in humans and dogs.

Similarities and Differences in the Biology of Aging

What do we mean by aging? There are numerous ways to define just what we mean by aging (also commonly known as senescence). Here, we define aging as the intrinsic physiological decline that occurs as organisms age, leading to a decline in fertility and fecundity, and an age-related increase in the risk of morbidity and mortality (3). As we mentioned above, age is the single greatest risk factor for most major causes of mortality in adults. This is shown in **Figure 1**, which illustrates that the age-specific increase in risk is exponential (linear on a logarithmic scale) for the major causes of human mortality in the United States.

While not all species suffer from the same diseases, everyone eventually dies. The way that age affects the risk of death shows striking similarities across almost all animal species (5–7). The risk of dying is typically high immediately after birth, declines to a minimum in early adulthood, and then begins to climb steadily, and like the pattern of individual diseases, increases exponentially. In humans, after age 30 the risk of death doubles about every 7–8 years (8). The shape of this relationship is notably similar in dogs (9). But there are important differences in the causes of this mortality. Some diseases, like cancer, are relatively common causes of mortality in both species, and increase with age not only in humans (**Figure 1**) but also in dogs (10–12). In contrast, while cardiovascular disease rises steadily to become the single greatest cause of mortality in humans (**Figure 1**), in dogs it appears to be rare, and independent of age (13, 14).

It is clear from these prior studies that both humans and dogs age, but *why* do species age? In the 1950's, Peter Medawar (15) and George Williams (16) laid out the evolutionary theory that explains why aging is inevitable. In short, if a germ-line mutation reduces fitness early in life, selection will tend to eliminate that mutation. But if that same effect is limited to later in life, selection will be relatively ineffective at weeding out the mutation. Over evolutionary time, these late-acting deleterious mutations will accumulate so populations will tend to carry large numbers of these variants, leading to senescent decline. And indeed, in almost every species examined, in the lab and in the wild, we see signs of aging (6, 17).

Interestingly, not only are the demographic patterns of aging conserved. The pathophysiological consequences of aging are also strikingly similar throughout the animal kingdom, from shortened telomeres, to mitochondrial dysfunction, to loss of the ability to maintain protein structure, and more (18). Turning from the consequences of aging to the molecular causes, over the past 30 years, researchers have identified a number of

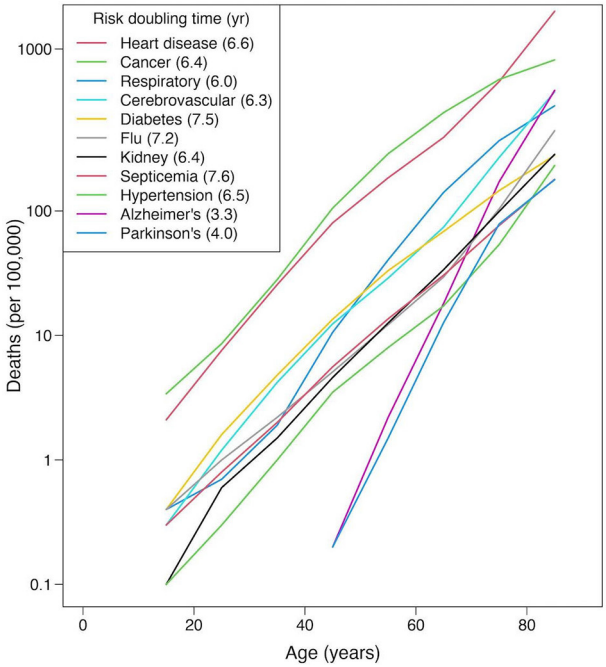

FIGURE 1 | Annual risk for diverse causes of mortality, based on 2013 US Centers for Disease Control National Vital Statistics Report. Note for virtually every major cause of mortality, risk increases exponentially with age (a straight line on a log-linear plot). The inset legend includes the mortality rate doubling time-the number of years it takes to increase mortality risk m to 2 m (4).

pathways which, when altered through drugs, diet, or genetic engineering, increase lifespan and healthspan in diverse lab organisms, including yeast, nematode worms, fruit flies and mice (19, 20).

These are exciting discoveries, but it remains to be seen whether these molecular pathways discovered in the lab can also explain variation in aging and age-related traits that we observe in the real world. In populations outside of the lab, the differences we observe among individuals—height, shape, behavior, age-specific risk of disease—are due to differences in genotype, and in the environments that they experience from the moment of conception and throughout their life. In fact, quantitative genetics teaches us that within a population, all of the variation that we observe for any of these traits, or *phenotypes* (**P**), is due to the sum of the genetic (**G**) and environmental (**E**) variation, and the interaction between the two: $\mathbf{P} = \mathbf{G} + \mathbf{E} + \text{cov}(\mathbf{G}, \mathbf{E})$.

To tease apart the complex network of mechanisms by which **G** and **E** ultimately shape aging-related traits, we have been led to consider companion dogs. We are motivated to think about aging in dogs not simply because of their physical proximity to us, but also because they show the most variability of any mammal, not only for morphology and behavior (21), but also for patterns of morbidity and mortality (13). From the smallest to largest breeds, size differs by more than 50-fold (22), and this dramatic size variation is closely related to lifespan, with large-breed dogs typically much shorter-lived than small-breed dogs (23). Given

that dogs and humans both have considerable genetic variation, many similarities in disease, and a shared environment, with their much shorter lifespan, dogs provide us with an excellent opportunity to transfer lab discoveries to the "real world." And given the much shorter lifespan in dogs, we might be able to more easily tease apart how genes and environment shape aging in dogs than in humans.

We are just at the beginning of this work whose goal is to uncover the causes and consequences of aging in dogs (24, 25). These studies are made possible not only by the nature of how dogs age, but also by the close relationship dogs have with their owners, who generously share these data with the researchers. These studies are just one small example of the incredibly rich nature of human-animal interaction, and the relationships it can lead to, in which aging is a central component. This leads to many fascinating questions about the ways that aging in both dogs and humans shaped the nature of this complex bond. In the following sections, we explore this in detail.

Aging and Human-Animal Interaction

Sharing our lives with pets is a global phenomenon and has been a central feature of human society for thousands of years (26). An increasing body of evidence indicates that pets provide us with physical and emotional benefits (27–29). They encourage us to be more active, make us laugh, provide comfort and affection, help us feel safer, and can even help us connect with our neighbors and make new friends. This companionship may be especially important for older adults as their social networks shrink. As we describe above, for many of us, our companion dogs provide us with our first direct and intimate experience of aging. Even as children, many of us first experience the challenges and gifts of caring for an older individual, and of navigating the emotionally and psychologically difficult terrain around end-of-life care through pet ownership [e.g., (30)].

Since older humans and dogs are both subject to psychological and physical changes as they age, it is important to find creative ways to address the health needs of both these populations. As we develop ever more sophisticated ways to define healthy or unhealthy aging in our companion dogs, what we learn is likely to translate to humans as well. For example, in looking for environmental determinants of healthy aging, given the relatively short lifespan of dogs, we might observe the impact of both beneficial and detrimental environmental factors on aging in dogs long before similar impacts would appear in humans. In this sense, dogs could serve as sentinels of environmental factors that might increase or decrease our own healthy lifespan (31).

Causes and Consequences of Aging

How can we understand the enormous variation in patterns of aging? Research on human aging has sought first to measure variation in lifespan, and then to measure the degree to which this variation is explained by genes and environment. It turns out that about 20–30% of the variation in human lifespan is due to genetic factors [(32, 33), but see (34)]. So it pays to have long-lived grandparents, but environmental factors make a big difference. The next step has been to identify which genes, and what environmental factors, contribute most to lifespan and age-related traits. In humans, one gene in particular, *ApoE*, has been shown to be associated with lifespan in studies of many different populations. There are particular alleles of this gene that are associated both with high risk of Alzheimer's Disease and short lifespan. Notably few other genes have been found in these studies.

There are considerable challenges in finding the many genetic and environmental factors that contribute to variation in aging. In particular, many genes that affect aging have extremely small effects, and so are hard to identify in even the largest studies (35). But humans are also hard to study because they live for so long. We have learned a great deal from numerous long-term longitudinal studies of human aging [e.g., (36–38)], but because we live so long, these studies take a long time—certainly longer than the duration of a graduate student or post-doc, and even the career of a scientist, interested in aging studies.

With this in mind, researchers have turned to the dog as a powerful model system to study aging in a natural population. As we mentioned above, dogs share similar mortality trajectories as humans, and similar pathophysiological processes (13, 14). Moreover, they share our environment, and so are likely to have at least some environmental risk factors in common with humans.

The first large-scale studies on dog aging have relied on retrospective analysis of existing data. These studies have provided overviews of the variation in lifespan among breeds, and the effect of size, age, and inbreeding on risk of disease and death (13, 14, 39–43). Researchers have also sought to identify genes associated with lifespan in dogs (44, 45). Given the close correlation between size and lifespan, it is particularly challenging to disentangle the two. For example, size in dogs is influenced by many genes, with one particular gene, Insulin-like Growth Factor 1 (IGF1), playing a major role. Large- and giant-breed dogs tend to carry two copies of the ancestral (wolf-like) IGF1 allele, while toy breeds tend to have two copies of a derived allele. Notably, IGF1 is also associated with lifespan in laboratory studies (46) and even in some human populations (47, 48). This has led some to suggest that large-breed dogs are short lived because of the IGF1 allele they carry. While the frequency of the large-size IGF1 allele is associated with shorter mean lifespan across breeds, we do not yet know if there is a causal relationship.

To fully understand how genes and environment shape patterns of aging, the gold standard is the long-term longitudinal study. Human cohort studies around the world have taught us much about genetic and environmental risk factors for a whole range of diseases [e.g., (36–38)]. Among the very many lessons learned, these longitudinal studies have taught us that smoking increases the risk of stroke (49), that a diet rich in fruits and vegetables promotes healthy aging (50), and that early-life socioeconomic status impacts late-life health (51). Dozens of cohort studies support the benefits of both non-vigorous and vigorous exercise in reducing overall mortality risk (52, 53). This latter finding has led many to consider that the potential

benefits of dog ownership for older people may be due to increased frequency and/or duration of exercise. We explore this further below.

Inspired by what we know about variation in aging in dogs, and by the success of human cohort studies, more recently, researchers have initiated large-scale longitudinal studies, setting out to follow thousands of companion dogs throughout their lives. The Golden Retriever Lifetime Study (GRLS) (24) is designed to better understanding the underlying causal mechanisms for variation in cancer in that breed, and the Dog Aging Project (DAP) (25) has set out to understand the genetic and environmental determinants of healthy aging by studying all breeds. These and several other ongoing large-scale studies in dogs (54–57) benefit from the power of community science, where dog owners in the general community generously share data about their dogs with researchers, with potential benefits to people, to dogs, and to science. Despite the sophisticated health care system to which many dogs have access, we know relatively little about what healthy aging looks like in dogs. As with human medicine, there are many veterinary specialties, but geriatrics is not among them. Projects like GRLS and DAP will provide the data needed to better understand what healthy aging looks like in dogs, what factors are most likely to promote healthy aging, and whether these findings can be translated to human populations.

This paper explores the current research into aging in both people and companion dogs, and in particular, how the relationship between older adults and dogs impacts healthy, active aging for both parties. The human-dog relationship faces many challenges as dogs and people age. In recent years, the field of aging has emphasized not just lifespan, but healthspan—the period of healthy, active lifespan. This focus on healthy, active aging is reflected in the World Health Organization's (WHO) initiative for a decade of focus on healthy aging (58) and recent initiatives from the US Surgeon General on Healthy Aging in Action (59). As owners age, dogs may be particularly important for maintaining social connection with others, heart health, mobility and even cognitive function. However, older adults may reach a stage of decline when they can no longer adequately care for their dog. Aging dogs may place additional demands and costs on their owner.

Healthy Active Human Aging

Life expectancy is increasing in many parts of the world and with that come new opportunities but also unprecedented challenges. Healthy aging provides the opportunity for older people to take an active part in society and enjoy an independent and high quality of life for longer. The WHO defines *healthy aging* "as the process of developing and maintaining the functional ability that enables wellbeing in older age" and it defines *functional ability* as being "about having the capabilities that enable all people to be and do what they have reason to value" (60). Given the rapidly growing number of older adults in the coming decades (61), innovative approaches to promote healthy aging are increasingly important. Extending the period of independent living in older adults can have a positive impact on quality of life and healthcare costs.

THE ROLE OF PETS IN HEALTHY ACTIVE HUMAN AGING

Our world is changing, and as populations become increasingly aged in many countries, communities need to be better able to support this societal shift. New, innovative approaches to help older adults remain healthier for longer as they age may extend their healthspan but also potentially reduce the burden of healthcare costs (62). The role that pets play in creating healthier, more engaged communities should not be overlooked. There is an increasing body of evidence suggesting that pets may offer a range of health benefits supporting older adults to retain their physical and mental health, independence, social connectedness and engagement (63–66). Pets also offer humans opportunities to nurture and feel needed, to provide a purpose, structure and routine for daily life (67), to enhance feelings of security (68), to give and receive affection, and to maintain older adults' ability to care for themselves independently (69).

Beyond physical benefits, pets may help us meet our basic need to connect with "another." Pets can provide a reason to get out of bed in the morning, a partner for walks through the neighborhood, and a positive topic of conversation with friends and neighbors. Opportunities to provide nurturance to others and to give and receive affection may decrease as we age, but pets are constant companions who can make us feel needed, valued, and loved. Several studies have shown that pets can often fulfill the four roles of an attachment figure proposed by Ainsworth (70). Specifically, many pet owners report that their pets are enjoyable and comforting (71), missed when absent (72), and sought out in times of distress (73).

Physical Health and Mobility

Exercising in later life can be a challenge despite its well-known benefits (59). In the U.K., only one in four people aged between 65 and 74 exercise regularly (74). By age 75, about one in three men and one in two women in the US engage in no physical activity (https://www.cdc.gov/physicalactivity). Adults aged over 50 years who frequently walked their dog were more likely to report having a sense of community, more likely to achieve the recommended levels of physical activity (at least 150 min/week), and less likely to be sedentary than those who did not live with a dog (75–80). In one study, they achieved an average of 22 additional minutes of walking per day (∼2,760 steps), compared to non-dog owners (74). Results from the Health & Retirement Study's longitudinal survey indicated that dog walking was associated with more frequent moderate and vigorous exercise, lower body mass index, fewer limitations in activities of daily living and fewer doctor visits (81). Dog owners walked faster and were more likely to maintain their walking speed over a 3-year study than dog owners who did not walk their dog or non-owners (82). Walking speed is thought to be an indicator of balance, and for older adults, balance is crucial for preventing falls and maintaining independence (83).

The American Heart Association has issued a statement in support of the role that dog ownership can play in reducing the risk of developing cardiovascular disease (CVD) (84): "Pet

ownership, particularly dog ownership, is probably associated with decreased cardiovascular disease" and "…may have some causal role in reducing CVD risk." One landmark study determined that risk of death from cardiovascular disease was decreased by 26% for pet owners compared to non-pet owners (85) following a serious heart attack, a result that was later replicated in larger cohort studies (86, 87). Presence of pet was associated with lower blood pressure in older adult patients with hypertension (88).

Socio-Emotional and Cognitive Health

The increased risk of isolation and loneliness in older adults has a profound impact on health and well-being, and is often associated with depression (89, 90), lower overall life satisfaction (91), and with reductions in mobility and activities of daily living (91, 92). The effect of loneliness and isolation on mortality is comparable to the impact of well-known risk factors such as obesity and smoking cigarettes (93). In a meta-analysis of 70 studies, the likelihood of death was 26% higher for those reporting loneliness, 29% higher for those experiencing social isolation, and 32% higher for those living alone (94). Pets can make us feel needed and valued. Older adults having contact with dogs reported reduced levels of loneliness and improved mental functioning (95), although some studies of loneliness showed little effect of interaction with dogs. It may be that some pet owners are lonely people who get a dog to alleviate loneliness while for others, dogs may be a protective factor against loneliness developing. Pet ownership is not a homogenous experience, which may explain the mixed results in studies of the impact of dogs on loneliness. Randomized controlled trials are needed to more definitively establish the relationship between pet ownership and loneliness (66).

Other socio-emotional benefits of human-dog interaction reported include older adults with dementia showing significant decreases in agitated behavior and increases in social interaction when a pet visited (96, 97). Pet ownership was associated with less depression following spousal bereavement (98).

A recent systematic review evaluated 145 research studies on the topics of human-animal interaction and physical health and exercise, depression and anxiety, and loneliness and social functioning in older adults (66). Among the less robust studies reviewed, pet attachment was associated with reduced loneliness in older adults, mediated the relationship between loneliness and health, and was viewed as a coping resource for loneliness. In contrast, most of the higher quality studies indicated no positive effect of pet ownership. However, one study found that individuals over 60 who lived alone reported their pets as particularly effective in attenuating loneliness and another found that higher levels of pet attachment related to less loneliness.

Pets as Social Capital

Social Capital is a concept that captures trust between people (including those we do not know personally), networks of social support, the exchange of favors with neighbors and civic engagement. Many studies show that Social Capital is positively associated with important social indicators including mental health, education, crime deterrence and community safety. Pet Ownership, particularly dog ownership, is linked to higher levels of social capital and civic engagement (99). In a larger study, over 2,500 pet owners and non-pet owners were surveyed across four cities (Perth in Australia and San Diego, Portland and Nashville in the US) reasonably comparable in size, urban density and climate (100). In all four cities, pet ownership was significantly associated with higher social capital compared with not owning a pet. This held true after adjusting for a raft of demographic factors that might influence people's connections in their neighborhood. Among Pet Owners of all types, social capital was highest in dog owners who walked their dog. Dog owners were twice as likely as non-pet owners to have gotten to know someone in their neighborhood (101).

Approximately 40% of pet owners reported receiving social support from people they met through their pet (101). Impact of pets goes beyond individuals. Emerging evidence indicates that pets may act as a social bridge between people and contribute to "ties that bind" societies and communities together, contributing to a civil society and healthy lifestyle. Pet owners were also more likely to be concerned about and active in their communities (101).

Not everyone wants a pet or indeed probably should have a pet. But given pet ownership is common, it should not be overlooked as a means of potentially strengthening communities. It follows that cities and neighborhoods should be "pet-friendly" to encourage responsible pet ownership. "No Pet" clauses in rental or social housing have been a strong barrier for pet ownership but recently we are seeing a change in some countries. For example, the UK government's Model Tenancy Agreement (102) includes provision for pets.

HEALTHY ACTIVE CANINE AGING

The burden of caring for an elderly pet can be particularly challenging for an elderly owner. Thus, maximizing healthy aging in dogs can improve quality of life not just for the dog, but also for the aging owner. And the goal is not simply to maximize longevity, which could lead to extended periods of poor-quality life with high morbidity, but rather to maximize the period of healthy lifespan, or "healthspan" (103, 104). In recent years, this same notion has been introduced into the canine literature (14, 25, 105).

As any dog owner knows, like humans, dogs slow down as they age. With age comes not only decreased mobility (106–108), but also changes in diverse behaviors (109, 110), age-related loss of cognitive function that, in many ways, mirror those in humans (57, 111), declines in physiological function (112) and increases in the risk of morbidity (13) and overall mortality (9, 42, 43).

Decades of epidemiological studies have shown us what we can do to maximize our own healthspan—eat healthy foods and in moderation, do not smoke, get plenty of exercise. And as we mentioned above, having long-lived parents and grandparents helps too. What about dogs? We know that genetics plays a major role in determining life expectancy in dogs, with small breeds typically living considerably longer than most large breeds (113). But we know surprisingly little about the effects of diet, exercise or other environmental factors on canine healthspan.

We do know a considerable amount about diet and health in dogs, though there are few carefully designed clinical studies focused on diet and age-related disease or longevity [e.g., (114)]. Inspired by decades of studies in laboratory organisms showing that dietary restriction can enhance healthy lifespan (115, 116), a long-term study of diet restriction in a colony of Golden Retrievers suggested that the same might be true in dogs (117, 118), though the effects in this study appear to be due primarily to increased adverse effects of osteoarthritis in *ad libitum* fed dogs.

The literature on how diet might maximize healthy aging in dogs is permeated with anecdotal claims and is in need of large-scale long-term studies. Where we see more consistency is in the literature on the risks of obesity in dogs (119). Obesity is most notably associated with increased problems with osteoarthritis in dogs, but also can affect overall quality of life (120). But here, too, more studies are needed to better understand if and how obesity might impact other health risks in dogs (121). Moreover, while we know that exercise is associated with decreased risk of obesity [e.g., (122)], to our knowledge no one has yet shown that exercise in dogs is associated with increased healthspan.

Given the impact of aging in the lives of both dogs and their owners, it is notable that while veterinary medicine, like human medicine, has a broad set of specialties, such as cardiology, oncology, parasitology, nutrition, and so forth, notably missing from the list is geriatrics. Dog owners and veterinarians alike can recognize an older dog, and the infirmities that come with age. But the in-depth knowledge of aging that a human geriatrician possesses does not yet exist in the veterinary medical landscape. With studies like the Dog Aging Project (25) and the Golden Retriever Lifetime Study (24) now underway, data from these studies should reveal the factors that influence risks of aging and age-related disease, the diagnostic parameters and particular treatments that might be most appropriate for older dogs, and finally, ways to increase healthspan in dogs.

ADVANCING RESEARCH ON OLDER ADULTS AND PETS

As we described above, we are now seeing well-funded, large-scale studies of aging in dogs (24, 25, 54–57). These studies complement the many ongoing studies in human populations. At the same time, the call continues for high quality, well-designed research on the special bond between older adults and pets as a means of improving human health in a rapidly aging world. Research questions need to move beyond pet ownership as a binary question and should be framed to examine different variables including: the extent and quality of regular interaction with dogs; pet keeping history over a person's lifetime; the length of time they have had a relationship with their current dog; contact with other people's dogs or through animal-assisted interventions; and importantly, the relationship between a person's desire for, and the reality of, pet interaction as a factor in observed human health outcomes (123). Priorities include how human-animal interaction (HAI) impacts on major transitions or events in the lives of older adults such as retirement, the death of a spouse, and seeking or moving from independent living into sheltered accommodation or an institutionalized facility (67, 124). Recent systematic reviews within sub-populations are welcome but more research is needed on more ethnically and culturally diverse populations (125).

High quality, well-designed research requires standardized measures that are well-validated so that different research studies can be compared; well-designed research with comparison groups and adequate sample sizes; a focus on specific outcomes; and longitudinal studies to understand the value of pets to healthy aging (66, 126, 127).

In their Consensus statement (124) the NIH reported the "need to recognize the heterogeneity of the older population and the complexity of the human-animal bond. … There is a need to specify the meaning of pets in everyday life and to explore the ways in which the presence of pets can affect the health and well-being of different segments of the older population" (128).

In addition to the call for more research, the development of special pet-care programs and services for and by older adults is recommended together with the implementation of protocols and guidelines for the admission of pets and visiting dogs to assisted living and institutionalized care settings (67).

Challenges and Potential Solutions to Owning Dogs for Older Adults

Many studies have shown benefits of dog ownership for older adults. Unfortunately, many are denied this pleasure because of negative attitudes and perceived obstacles by the person themselves [e.g., the inconvenience of pet care or restrictions on freedom to travel, (129)] or their family, carers or health professionals concerned about the financial cost, the risk of zoonoses, infections or extra workload (67). Pet ownership declines with age—nearly 40% of adults in the US aged 50–67 have a pet but this declines to only 9% for those aged 68 and over (130). Many of these risks are relatively small. The risk of zoonotic infection is small other than to certain particularly vulnerable populations (67). Common concerns and barriers related to pet ownership include finances, functional capability to meet the pet's needs, restrictions imposed by their living arrangements and concerns should the pet owner fall ill or die (67, 131).

Some concerns may be relatively easily overcome with extra support from family or carers, or from external services, although there may be an associated cost. So how can older adults be supported to maintain or initiate responsible pet ownership to enjoy the companionship and health benefits dogs may bring, or to find alternative ways of interacting with dogs without the responsibility of owning a dog?

As older adults age they may become physically weaker, which may compromise their ability to interact with and adequately care for their dog (67, 127, 131). Heart and lung disease, osteoarthritis, or loss of sight may compromise their ability to adequately exercise their dog (127) or manage the motor skills necessary for attaching leads, lifting pet food or driving their dog to vet appointments or to the dog park. Older adults with dementia, still

living independently, may lack the planning, organizational, and memory skills to safely care for a dog (127).

Addressing these concerns and potential barriers requires education of older adults about responsible pet ownership and welfare standards for animals kept as companions. Talking about budget, future plans and health with older adults interested in getting a pet will help them and their families and carers make good decisions (e.g., appropriate pets for their lifestyle and health status; basic discussions about exercise needs and financial resources needed to adequately care for the pet; decisions about care of the dog if the older person can no longer adequately care for their pet or they have died). Resources on how to re-home a pet safely if needed should be shared to plan for a time when they may no longer be able to meet the needs of their pet. Potential or aging owners should be made aware of existing programs that would enable them to interact with pets without having the responsibilities involved with owning them (e.g., participation in socialization programs for shelter pets, fostering shelter dogs, or keeping a dog company while friends, neighbors, or relatives are away from home working or traveling) (132).

Dog walking in particular, may be especially relevant for older adults. Maintaining physical functioning as we age is critical to maintaining independence and preventing the move from independent living to nursing homes (83). If an older person is no longer able to adequately care for a dog, they may still be able to have contact with dogs through informal dog walking groups or by walking "loaner dogs" or local shelter dogs (64). Pet visitation programs are offered in some day centers, seniors residential homes, hospitals and hospices. Some older adults may be referred for canine therapeutic programs, which support maintenance of functionality (133), orpartnered with social care providers (e.g., Meals on Wheels for their Pet Feeding programs). Increasingly, dog cafes and dog date programs are being set up to connect lonely people with dogs who enjoy human attention (134, 135).

The challenges of caring for a dog as an owner ages are compounded when older adults' dogs themselves age and require more medical attention and care. As dogs age, their declining health and strength can impact the relationship with their owner, the health benefits they can bring to the owner and the enjoyment of dog ownership. For example, sensory loss, osteoarthritis and other conditions can affect canine mobility, cognitive function and ability to locate, attend, engage and move comfortably. Walks may become less enjoyable as dogs slow down or struggle to walk on rough ground (136). Aging owners may struggle to carry their dog if it can no longer navigate stairs or steps to go outside (67).

There are clearly many challenges, but we also see exciting opportunities. As we mentioned at the beginning of this article, thinking about issues related to aging creates the opportunity for conceptually innovative interdisciplinary thinking. As we age, our companion dogs might help us to better understand and better cope with the physical challenges that we face. At the same time, our aging companion dogs create a living laboratory in which we can learn to work through challenging social and philosophical problems that we might also face with our loved ones and ourselves. How do we weight economic costs in decisions about late-life health care? How do we prioritize maximizing healthspan vs. lifespan, and how do we work through decisions that require prioritizing one over the other? What do we do with a sick pet when the effect of the treatment might be harder to bear than the disease? And how do we make the wisest choices around end-of-life/palliative care in our pets?

DISCUSSION

The need remains for high quality research that examines specific sub-populations of older adults. Research findings are currently mixed but we have an encouraging foundation on which to build. We know enough, and we owe it to the millions of older adults, to collectively engage and mobilize their stakeholders with the promise of science to potentially benefit many lives. The call for more, better quality HAI research has been heard before (127). There remain questions about the efficacy of Animal-Assisted Interventions and which are the most effective elements, about dosage, the time course of effects, the populations most likely to benefit and the role of lifetime pet ownership/interaction history. The National Institutes of Health/Mars Inc. Public-Private Partnership has shown the impact a concerted focus can have on a specific area of HAI research (125), not only in terms of funding, but also in guiding key stakeholders as to what to focus on and how to prioritize research topics. A similar focus is needed for older adults. New initiatives such as the Consortium on Social Isolation and Companion Animals (137) have made a good start on bringing together researchers and other stakeholders but the need remains for greater, sustained funding and research support of this area, which has so much potential to improve human health in a rapidly aging world.

AUTHOR CONTRIBUTIONS

SM and DP helped conceive, outline, write, and edit this manuscript. Both authors contributed to the article and approved the submitted version.

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The Indispensable Dog

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Dogs' remarkable success in living in a human-dominated world rests on a set of adaptations to cohabitation with humans. In this paper, I review the nature of these adaptations. They include changes in reproductive and foraging behavior from their ancestor species, wolves, which can be understood as adaptations to the change from hunting live prey to feeding on human food residues. Dogs also show several changes in social behavior which are more controversial and even somewhat paradoxical. Contrary to theories of canine domestication which view dogs as less aggressive and more cooperative than wolves, several studies show that dogs' social interactions with conspecifics are more hierarchical and competitive than are wolves'. As scavengers rather than hunters, dogs do not need to cooperate with conspecifics the way that wolves do. But how then can we understand dogs' willingness to cooperate with humans? I propose an integrated account of dogs' social behavior that does not assume that dogs need to recognize the species-identity of the individuals with whom they interact. Because of the overlap in formal signals of dominance and submission between dog and human and people's complete control over the resources dogs need, I propose that people occupy a status of "super-dominance" over dogs. This conception suggests several new lines of research which could shed light on the human-dog relationship to the benefit of both partners.

Keywords: domestication, symbiosis, dominance, social hierarchy, dogs (*Canis lupus familiaris*), wolves (*Canis lupus lupus*)

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INTRODUCTION

Dogs (*Canis lupus familiaris*) are by any measure exceptional beings. They are the most widespread large mammal (after humans) on this planet. The total world population of dogs is estimated to be around 800 million individuals (Hughes and Macdonald, 2013; Rowan, 2020), and dogs are present on every continent except Antarctica (there were dogs on Antarctica too until they were banned in 1994: British Antarctic Survey, n.d.). Dogs are the most phenotypically diverse mammal (Wayne, 1986) and were the first domesticated organism, arising from wolves (*Canis lupus lupus*) over 15,000 years ago – millennia before any other animal or plant was domesticated (Larson et al., 2012). Dogs live alongside people in a high state of intimacy. For example, over 50% of adult women respondents to a survey in the United States reported that they let their dogs sleep on their beds with them (Hoffman et al., 2018: it should be noted that the participants were self-selected and unlikely to be representative of the broader population; however, no better study is available). Some authors (e.g., Coppinger and Coppinger, 2002) have argued that this level of intimacy is a recent phenomenon, but, although the proportion of people living so intimately with dogs may have increased over the

last two centuries (e.g., Ritvo, 1987), in a discussion of how to keep dogs written by an Ancient Greek nearly two millennia ago, the author advocates, "… it is best for (dogs) to sleep with men:- as they become thereby affectionately attached—pleased with the contact of the human body, and as fond of their bedfellow as of their feeder." [Arrian, 1831, pp. 93–94 (original second century CE)]. The archeological record provides many forms of evidence that people and dogs have long lived in close connection with each other (Sykes et al., 2020).

Clearly, the remarkable success of dogs is due in some sense to their adaptations to human proximity. Dogs are obligatory human symbionts (Coppinger and Coppinger, 2002). That is to say, dogs are found living close by humans and dependent on food sources they obtain from humans. In the first world, this provisioning is mostly intentional: In the developing world, the provisioning is more often unintentional as when dogs scavenge on human refuse (Butler and du Toit, 2002; Coppinger and Coppinger, 2002). Few dogs survive entirely by hunting live prey, and there is no evidence of populations of dogs that are self-sustaining entirely by this method of foraging (Coppinger and Feinstein, 2015; Dingoes would be the one clear exception to this rule, if one considers dingoes to be dogs: Smith et al., 2019, but see also Jackson et al., 2019).

The importance of adapting to human proximity may be central to dog's success in the human-dominated world, but the essence of that successful adaptation remains a topic of continuing debate and controversy in the literature. In this paper, I will restrict my discussion to aspects of dog behavioral adaptation to the human niche that are well established and consider what conclusions can be drawn from these facts.

REPRODUCTIVE BEHAVIOR

Modern dogs have notably more fluid reproductive behavior compared to their ancestors, wolves (*Canis lupus lupus*). Where wolves form pair bonds which can be lifelong, do not become reproductively active before the second year of life, have a rigid breeding season, and produce no more than one litter of pups per year (Rausch, 1967; Kleiman and Eisenberg, 1973; Macdonald and Moehlman, 1982; Haase, 2000; Mech, 2002), dogs are already reproductively active in their first year of life (Ghosh et al., 1984; Wandeler et al., 1993; Boitani and Ciucci, 1995; Lord et al., 2013). Female dogs may show preferences for certain mates and are not technically promiscuous, but they usually have multiple mating partners (Pal, 1999; Cafazzo et al., 2014). There is at least one report of male dogs guarding their mates through pregnancy and nursing (Pal, 2005), but in general, dog fathers do not contribute to the support of their mates or offspring (Lord et al., 2013 and references therein). Female dogs reproduce on average every 7 months throughout the year (Macdonald and Carr, 1995; Boitani et al., 2007), though seasonality in response to resource availability is possible, as in India, for example, where mating occurs in winter so that pups are born in the late monsoon season (Oppenheimer and Oppenheimer, 1975; Pal, 2001; Chawla and Reece, 2002; Pal, 2008). Unlike in wolves, males are continuously reproductively active (Gipson et al., 1975; Haase, 2000; Lord et al., 2013).

Both wolf parents collaborate to raise their pups; pups which may not leave their parents' family group until the second year of life (Rausch, 1967; Mech, 1981; Peterson et al., 1984). By contrast, dog pups are nursed by their mother for 5 to 11 weeks (Martins, 1949, Scott and Fuller, 1974, Pal, 2001, 2008) and thereafter must survive on their own. There are sporadic reports of fathers regurgitating for their young (Malm, 1995; Pal, 2005; Paul et al., 2014) as well as playing and protecting them (Pal, 2005; Paul et al., 2014), but support from the father or young of earlier litters does not appear to be the norm (Martins, 1949; Mech and Boitani, 2003; Pal, 2008; Bonanni and Cafazzo, 2014). There are also reports of allonursing by females denning together (Daniels and Bekoff, 1989; Pal, 2005; Paul et al., 2014), but group denning does not appear to be widespread.

FORAGING BEHAVIOR

The quite distinct reproductive behaviors of wolves and dogs are clearly adaptations to their different foraging niches (Marshall-Pescini et al., 2017a). Wolves survive by hunting live prey which is larger than they are and is highly motivated not to become a wolf's dinner. This can only be achieved by a close-knit group of individuals who have undergone a form of apprenticeship which can take from 1 to 3 years (Mech, 1981). Hunting for wolves is so complex that they tend to specialize on a subset of available prey species and interbreed preferentially among conspecifics who focus on the same prey species (Pilot et al., 2012). Wolf hunting success is dependent on group membership. For easier to kill prey, such as elk (*Cervus elaphus*), hunting reaches an optimum for groups of two to six wolves; for bison (*Bison bison*), which are far more challenging prey, capture success only levels off at groups sizes of 9 to 13 individuals (MacNulty et al., 2014).

The primary form of foraging for dogs is scavenging. The majority of the world's dogs subsist on food remains discarded by humans (Boitani and Ciucci, 1995; Butler and du Toit, 2002; Bhadra, 2014; Coppinger and Feinstein, 2015), and even pet dogs fed directly by people are still technically scavenging in so far as the food given them is primarily either surplus to the human's requirements or manufactured from "animal by-products" which are portions of meat animals that people prefer not to eat (What are animal by-products? n.d.). Dogs are not typically successful hunters and there are few populations of dogs which survive and maintain numbers entirely by hunting (Coppinger and Feinstein, 2015). The scavenging niche does not require the complex skillset that hunting live prey demands. It hardly needs noting that extracting and consuming the remnants of already deceased and butchered prey is a far simpler procedure and does not usually benefit from the coordinated action of a group of closely attached individuals. Indeed, the presence of conspecifics leads to competition in

free-ranging dogs and they prefer to forage solitarily outside the mating season (Sen Majumder et al., 2014).

Dogs' foraging and reproductive behavior can be understood as an interlocked suite of adaptations to a novel niche. Wolves need to reproduce seasonally because their prey shows seasonal availability. Dogs do not (typically) need to constrain themselves to only reproduce at particular times of year because the availability of their diet usually varies little by season. Wolves need to form pair bonds and keep their young with them to ensure their survival during the early months of life and then to apprentice them in the complex task of hunting large live prey. Their assistance is important in the success of the hunt (Mech, 1981; MacNulty et al., 2014). Dogs, on the other hand, can forgo pair bonding because their young require little training. Around 8 weeks of age, pups start following their mother to food sources and may also beg for food from people (Macdonald and Carr, 1995; Pal, 2008; Lord et al., 2013). No further parental support is offered. The more flexible reproductive strategy of dogs enables them to respond to sudden changes in resource availability such as when, for example, a new human group moves into their territory, or the foraging success of their host human population suddenly improves.

SOCIAL BEHAVIOR

Both reproductive and foraging behavior include interaction with others and thus are forms of social behavior, but I now proceed to consider other aspects of social behavior in dogs. Like all social species, dog social behavior shows itself in interaction with conspecifics, but, unlike most species, dogs may also have important social interactions with members of other species. I consider these separately.

Conspecific Behavior

The behavior of dogs toward others of their species does not consistently indicate strong within-species bonds. Dog pups show distress if forcibly separated from their mother (Fredericson, 1952; Pettijohn et al., 1977) but the only available investigation of the impact of the separation of adult kennel mates did not find any detectable impact on behavior or stress hormone levels (Tuber et al., 1996).

In free-roaming dogs, a diversity of social patterns has been found at different study sites around the world. Free-ranging dogs have been reported to be solitary or dyadic in studies from India: (Sen Majumder et al., 2014), Zimbabwe (Butler et al., 2004), the United States (Beck, 1973; Rubin and Beck, 1982; Berman and Dunbar, 1983, Daniels, 1983; Daniels and Bekoff, 1989), and Ethiopia (Ortolani et al., 2009). However, several studies have found dogs in groups ranging from 6 to 28 individuals in India: (Sen Majumder et al., 2014), Italy (Macdonald and Carr, 1995; Bonanni and Cafazzo, 2014), and the United States (Beck, 1973; Gipson, 1983). It appears that the size of groups may depend on the availability of food, the breeding status of females, and the season (Sen Majumder et al., 2014). Living in larger groups may offer protection (Bhattacharjee et al., 2020) and larger groups may also be more successful at hunting (Butler et al., 2004; Vanak and Gompper, 2009; Bhadra, 2014).

Although it should be noted that the studies cited here were carried out by different researchers in very diverse parts of the world and over a considerable time range – so that the range of findings may be due to different methodologies – nonetheless, there is suggestive evidence that dogs can adapt their social structure to suit changing circumstances.

Hierarchical Social Organization

Hierarchical social structure is a common, but not inevitable, concomitant of living in social groups (Immelmann and Beer, 1992; Dugatkin, 2020). The question of whether dogs live in hierarchical social groups, with the relativities of status for individuals which that implies, has become controversial in recent years because of the misuse of the term "dominance" by certain popular dog trainers, such as Millan and Peltier (2007), Fincke (2004–2016), and the Monks of New Skete (2002). These individuals use "dominance" as a cover for painful and regressive forms of animal training (Yin, 2007; American Veterinary Society of Animal Behavior, 2008; Bradshaw et al., 2009; McGreevy et al., 2012). This controversy has little to do with the use of "social dominance" in the strict ethological sense (Immelmann and Beer, 1992). Dominance in ethology is simply the tendency for certain individuals in a social group to have at least partially consistent preferential access to limited resources, such as shelter, food, and sexual partners (McFarland, 1987). Individuals with consistent access to constrained resources are known as "dominant": Those that consistently have less access to resources are "subordinate." Dominance hierarchies may form a consistent rank ordering, in which case Greek letters, alpha, beta, etc. are used to label individual positions with the hierarchy. The concept of dominance includes the enforcement of preferential access by aggression and agonistic interactions, but ethologists now also recognize that social hierarchies are commonly maintained by signals of superior and inferior status known as formal dominance and subordination signals (Peterson et al., 2002; Flack and de Waal, 2010). These formal signals are not in themselves aggressive or threatening but are understood by social interactors as indicating relative status, i.e., dominant or submissive.

Groups of free-living dogs have been found to live in social hierarchies in several studies including in Italy (Bonanni et al., 2010; Cafazzo et al., 2010; Bonanni et al., 2017; Silk et al., 2019), Spain (Font, 1987), and India (Pal et al., 1998; Sen Majumder et al., 2014). Social hierarchies have also been observed in owned dogs in the United States at a day care center (Trisko and Smuts, 2015) and a dog park (Bauer and Smuts, 2007). Furthermore, group-housed dogs studied in the Netherlands were found to experience social hierarchies (van der Borg et al., 2015).

The studies of free-living dogs in Italy found that dominant individuals had higher copulatory access (Cafazzo et al., 2014) and a higher likelihood of leading group movements than lower-ranking individuals (Bonanni et al., 2010). Silk et al. (2019)

studying a group of 25 to 40 free-ranging dogs in a suburb of Rome, identified that older and male animals were typically dominant over younger female ones.

Two studies have identified formal dominance signals in groups of dogs. Bauer and Smuts (2007) studied owned dogs at a park and found that, even as the playing dogs reversed many roles – including chasing and tackling – certain behaviors remained stable in dyads. These including mounting, muzzle biting, and licking – suggesting they were stable formal dominance-status markers. van der Borg et al. (2015), studying a group of 16 dogs living in kennels with outdoor group play opportunities, noted two behavioral markers of formal dominance: high posture and muzzle bite. Several behaviors also functioned as formal markers of submission: body tail wag, lowered posture, mouth lick, and pass under the head. These authors analyzed the dominance structure of the dog group as a whole and, using a scale developed in primate research which categorizes social structures on a scale from (1) despotic through (4) egalitarian (Flack and de Waal, 2010), determined that the dogs scored around (2) tolerant. The dogs showed a moderately steep social hierarchy with large asymmetries in formal signal use and mild to moderate levels of aggression.

Bradshaw et al. (2009) argued that dogs do not form social hierarchies and presented data from a group of neutered males in which, they argued, no overall social structure could be observed. Notwithstanding this claim, the data presented clearly showed that at least some of the dogs formed a linear hierarchy of dominance status. Schilder et al. (2014), commenting on these findings, suggested that a group of human-resourced, sterilized, animals all of the same sex may have had no resources to compete over and thus might not be expected to show much overt social hierarchy.

Boitani and Ciucci (1995; see also Van Kerkhove, 2004; Boitani et al., 2007) also suggested that dog groups lack clear hierarchies because they observed multiple breeding individuals – which would not be found in a wolf pack. However, Cafazzo et al. (2010) noted that social hierarchies can still be present, including preferential reproductive access, even if the overall mating system of a group tends toward promiscuity.

Bradshaw et al. (2009) further raised the objection that "dominance" is often mistakenly spoken of, particularly by naïve dog trainers, as if it was a personality dimension – a property of an individual rather than of the interactions among individuals. Although it is true that dominance relations are defined by interaction, it is also the case that the nature of these interactions depends on certain relatively stable qualities of the interacting individuals. It is surely noteworthy that tests of dog personality or temperament currently in use have identified traits relevant to dominance and submission relationships. These include "submissiveness" (Jones and Gosling, 2005); "leader/dominant" (Ákos et al., 2014); and "boldness" (Svartberg et al., 2005).

The controversy over dominance in dogs is puzzling in so far as it has been known for many years that similarly raised groups of dogs show higher rates of conspecific aggression and competition than wolves (Frank and Frank, 1982; Feddersen-Petersen, 1991, 2007). Feddersen-Petersen (2004) even raised mixed groups of dogs (poodles) and wolves and found that, at 4 months of age, male poodles outranked the wolves in access to food and preferred locations.

More recent studies also show steeper social hierarchies in dogs than in wolves. Dale et al. (2016) gave similarly raised groups of dogs and wolves living in conspecific groups a carcass to feed on. Where subordinate wolves were able to feed to a similar level as their more dominant group-mates, dominant dogs monopolized the carcass at the expense of subordinate group members. Range et al. (2015) offered pairs of similarly raised dogs and wolves a food item that was large enough to be shared, but small enough to be monopolized by a dominant individual if it chose to do so. In the wolves, the dominant individuals tolerated their subordinate group-mates sharing food with them, whereas in dogs the dominant animals did not allow subordinate individuals to eat and subordinates did not even dare approach the food source.

Cooperation and Competition

In addition to their steep social hierarchies, dogs also show elevated levels of competition and have difficulty cooperating with conspecifics to solve tasks. Marshall-Pescini et al. (2017b) gave pairs of dogs and wolves from similarly raised groups a task in which the two animals had to pull on strings simultaneously for either of them to obtain a reward. Wolves were successful on the task but none of the dogs achieved any level of success. Ostojić and Clayton (2014) were able to demonstrate some success in dogs on this task by extensively pre-training the dogs. However, the dogs they tested were pets living together in human households where human intervention may have imposed levels of tolerance that the dogs left to themselves might not have developed (Marshall-Pescini et al., 2017b).

Bräuer et al. (2013, 2020) claimed to have demonstrated cooperation in pairs of pet dogs on a task where the dogs had to pass through one of two gateways in a barrier. However, this task is not a clear test of cooperation because each gateway was not wide enough or open long enough to permit two dogs to pass. Consequently, the dogs had to separate to pass through the gateways: One individual always had to wait for the other to pass through before its own gateway would open. Thus, the success of dogs on this task is in fact evidence of their reluctance to cooperate – in the strong sense of come together to work on a task together – rather than the opposite.

Although it may run against expectations based on interaction with household pets, there is abundant evidence in the scientific literature that dog groups can be very hierarchical, and dogs may be highly competitive and reluctant to share resources. Marshall-Pescini et al. (2017a) pointed out that, relative to their ancestors, wolves, dogs have less need to cooperate in their foraging and also cooperate less in raising young. Wolves have an essential need to cooperate with group members in order to kill the prey on which

they feed. Furthermore, the outcome of a successful hunt is usually more than an individual wolf can consume. Consequently, wolves have many motivations to cooperate in foraging and sharing the results of their kill. These factors that motivate cooperation in wolves have limited applicability for dogs who have less need either to cooperate in obtaining food or to share the results of their foraging.

Overall, there is plentiful evidence that the social structure of dogs is both more flexible than that of wolves, with groups varying in size from solitary individuals to more than two dozen, but also shows signs of more extreme social hierarchy. This flexibility of social group size presumably reflects the diversity of food sources and dangers that dogs face in different parts of the world (as well, possibly, as different study methods). The steeper social hierarchy found in dogs than wolves is more surprising and even counter-intuitive but may also be related to dogs' foraging strategy where cooperation is seldom needed, often counter-productive, and may have been selected against. To date, there do not appear to be any studies on the genetic relatedness of individuals within dog groups that might address the possibility of kin selection for altruistic and cooperative behavior.

Heterospecific Behavior

Dogs not only have social interactions with their own species but also can form social groups with members of other species including, most particularly, human beings.

Flight Distance

One simple behavioral measure of dogs' tolerance for human proximity is assayed as flight distance – the linear distance at which an individual flees from a gradually approaching human. Dogs reduced flight distance compared to wolves is surely a major component of their adaptation to living in proximity to humans and scavenging on human food remnants. For animals foraging on human trash dumps, flight distance to the approach of humans will be a key determinant of their extractive effectiveness.

Flight distance is defined as the distance from an intruder at which an individual flees (Immelmann and Beer, 1992). Wolves scavenging on human refuse in Scandinavia have been observed to have a flight distance to the human approach of around 200 m (Karlsson et al., 2007). Estimates of flight distance in dogs are quite varied, but all are considerably shorter than this estimate for wolves. Bonanni and Cafazzo (2014) reported flight distances of 20–50 m in free-ranging dogs in Rome, Italy. Ortolani et al. (2009) reported flight distances of around 5 m in free-ranging dogs around villages in rural Ethiopia. Although no formal data appear to be available, everyday experience indicates that the flight distances of pet dogs living in human homes are less than 1 m – if the concept of flight distance can be applied to these animals at all.

Attachment to Humans

As pet dogs are commonly spoken of as family members or friends to humans (Serpell, 2004), several investigators have adapted measures that are commonly used to study intimate relationships in human psychology to the study of dog-human relationships. Several studies have used a modification of a procedure commonly used to measure the strength of attachment between a child and his or her primary caregiver (usually the mother) – the strange situation procedure (SSP) developed by Ainsworth et al. (1970). In this test, a child is brought into an unfamiliar room with his mother. The child is briefly left in the room with a stranger; the mother returns, comforts the child and then leaves with the stranger so the child is briefly completely alone. Finally, the stranger returns, followed by the mother. Attachment is categorized on the basis of how the child reacts to being left alone and with the stranger and how he responds to being reunited with his mother (Ainsworth et al., 1978). Securely attached children are those who are happy to explore in their mother's presence and are distressed by her disappearance but show a willingness to be comforted quickly on her return.

Several studies, starting with Topál et al. (1998), have shown that many dogs tested in the SSP with their primary caregivers show secure attachment toward the humans they live with (e.g., Topál et al., 1998; Rehn et al., 2013; Thielke and Udell, 2019, 2020; Wanser and Udell, 2019; Wanser et al., 2020). Two additional observations in the SSP raise questions about how to understand this finding, however. First, Gácsi et al. (2001) found that dogs living in an animal shelter tested in the SSP with a person they had only interacted with three times for 10 minutes per session showed clear signs of attachment toward that person. Second, the only study that tested dogs in the SSP with another dog from the same household as "caregiver" (Mariti et al., 2014) found few signs of distress when the target dog was separated from its companion, and these dogs were, in fact, less stressed when left alone with an unfamiliar person than when they were in the company of the other dog.

A handful of studies have investigated hand-reared wolves' reactions to separation and reunion with familiar humans in the SSP. Topál et al. (2005) tested a group of hand-reared wolves at 16 weeks of age alongside a group of pet dogs of the same age. These authors found no signs of attachment to human caregivers in the wolves. In contrast, when Hall et al. (2015) tested hand-reared wolf pups at 3, 5, and 7 weeks of age, they found clearly differentiated responses to caregivers compared to strangers and strong responses to the reunion after separation, leading them to conclude that their wolf pups were securely attached to the caregivers. This pattern of results might suggest that hand-reared wolf pups show attachment to caregivers that fades as they grow older; however, Lenkei et al. (2020) tested adult wolves in the SSP and found secure attachment to human caregivers. Hall et al. (2015) suggested that Topál et al. (2005)'s failure to find secure attachment might have been due to the fact that the animals they tested were permanently removed from human homes between 2 and 4 months of age.

Taken together, the findings from hand-reared wolf pups and dogs tested in the SSP suggest that dogs may form secure attachments to human caregivers, but more rapidly than would

be expected in our own species. Wolves may also under certain conditions show secure attachment, but in their case, the conditions for this finding may be more limited. However, the restricted range of studies on hand-reared wolves means these conclusions must be approached with caution.

Other, somewhat simpler, tests have also demonstrated pet dogs' interest in their owners. Horn et al. (2013) presented pet dogs with a manipulative problem and compared how long they attempted to solve the task either with their owner in the room with them or on their own. The presence of the owner prompted the dogs to persist longer with the task than when left alone. Gácsi et al. (2013) found that dogs were less stressed when a stranger approached if they were with their owner than when alone. No equivalent tests appear to have been carried out on hand-reared wolves.

Jakovcevic, Mustaca, and Bentosela (2012) studied the bond between dog and human simply by measuring the latency to approach and proportion of a two-minute interval a dog would spend within 1-m of a seated person. Bentosela et al. (2016) extended this paradigm to hand-reared wolves and found that dogs had a considerably shorter latency to approach both familiar and unfamiliar seated humans than wolves and also spent more time within 1-m of the person.

Findings that pet dogs are disturbed by the sound of a human crying (Custance and Mayer, 2012; Yong and Ruffman, 2014) and will attempt to rescue their apparently trapped owner (Bourg et al., 2020) may also be viewed as evidence that pet dogs can become emotionally attached to people.

Cooperation With Humans

A variety of studies demonstrate that dogs readily attend and respond to human behavior. Pet dogs have been shown to beg from people who can see them in preference to people whose vision has been obscured in certain ways (Cooper et al., 2003; Gácsi et al., 2004; Udell et al., 2011). Udell et al. (2011) found that dogs only attended to forms of visual occlusion with which they had prior experience and hand-reared wolves were also sensitive to the implications of certain forms of obscuring of human vision. To date, studies of this type have not been attempted on dogs that were not living as pets in human households.

Wolves have been compared to dogs in tests of cooperation involving pulling on strings to obtain food. In studies, where food can only be obtained when two partners pull simultaneously on opposite ends of a string, hand-reared wolves have shown similar levels of cooperation with human partners as dogs (Range et al., 2019).

Several studies have demonstrated that pet dogs will follow human pointing gestures to find hidden food (e.g., Hare et al., 2002; Hare and Tomasello, 2005; Bräuer et al., 2006; Udell et al., 2008; Kaminski and Nitzschner, 2013). This ability has also been demonstrated in hand-reared wolves (Udell et al., 2008; Gácsi et al., 2009), and a recent review identified a wide range of both domesticated and non-domesticated species from diverse taxa which follow human pointing gestures given prior experience around people (Krause et al., 2018).

Dogs not living as pets in homes do not show the same level of success in following human pointing gestures. Reduced performance in the following points has been observed in street dogs in India (though see also Bhattacharjee et al., 2017, 2020, for evidence of successful point following in about half the street dogs approached), as well as kennel-living dogs (Udell et al., 2010; Lazarowski and Dorman, 2015).

The fact that dogs' success in attending to and following human actions depends on the individual dog's experiences around people, combined with the plentiful evidence that individuals from a wide range of species can also follow human gestures if they have had suitable ontogenetic experiences, indicates that dogs' readiness to cooperate with people is a consequence, rather than a cause, of their success in living alongside humans.

Summary on Heterospecific Behavior

Dogs' interactions with humans can be classified into two groups: the more emotional, attachment-like, patterns of behavior and the more cognitive or conditioned responses to specific human actions, such as pointing gestures. Emotional responses, including fear reactions as measured in flight distance, show differences between dogs and wolves with dogs much less fearful and more likely to form attachments to people than are wolves. On the other hand, reactions to discrete human actions do not appear to show the same kinds of differences between dogs and wolves.

CONCLUSION: DOGS' ADAPTATIONS TO HUMANS

Dogs' enormous success living in a human-dominated world rests on a set of adaptations to living in close proximity with our species. These include alterations in reproductive and foraging behavior from their ancestor species, wolves, which are readily understood as adaptations to the change from hunting live prey to scavenging on food residues that people offer – whether intentionally or not. The changes in dog social behavior are less obvious and indeed somewhat paradoxical. Contrary to theories of canine domestication which propose that dogs are less aggressive and more cooperative than wolves (e.g., Hare and colleagues' "Survival of the friendliest," Hare et al., 2002; Hare, 2017; Miklósi and Topál's "Inter-specific social competence" hypothesis Miklósi and Topál, 2013), in fact, several studies clearly show that dogs, in their interactions with members of their own (sub) species are in fact more competitive and aggressive than are wolves. A strict social hierarchy may be even more important to dogs since their food is often in small portions that cannot be shared, unlike the larger carcasses on which wolves often feed.

In itself, dogs' more competitive and hierarchical interactions with their own species are not inconsistent with their foraging niche. Dogs do not share wolves' need to cooperate to obtain or consume food (Marshall-Pescini et al., 2017a).

Placed alongside dogs' willingness to attend and cooperate with humans, however, it does present a paradox of sorts: How to conceive of dogs' different patterns of social behavior toward their own species on the one hand and humans on the other? It is implausible to propose that dogs have different programs of social behavior that they bring into play depending on the species identity of the social partners they are interacting with because no mechanism of species identification has ever been proposed. No mammal is born recognizing its own species – rather it develops an awareness of what kinds of individuals to have social relationships with during the critical period for social imprinting early in life (Hess, 1973). Furthermore, dogs do not just have social relationships with conspecifics and humans: They may also form social bonds with members of other species they interact with during the critical social imprinting period (Coppinger and Coppinger, 2002). Thus, livestock guarding dogs raised alongside sheep or goats will socially imprint on those species and socially interact with them through life. How does a dog know whether it should interact with sheep competitively – as it would with another dog, or cooperatively – as it would with a human? Clearly some more over-arching explanation is needed that does not assume that dogs identify diverse species and bring different social behavior patterns into play depending on that identification.

Range et al. (2019) suggested that dogs' behavior toward humans could be viewed as "deferential" and that this is then consistent with what they view as a "conflict-avoidant" pattern of social interaction with conspecifics. I have taken this valuable suggestion further and proposed that dogs' extreme sensitivity to hierarchy in social relationships may be the solution to the apparent paradox of their different behavior toward humans and conspecifics (Wynne, 2021). Several of the formal indicators of dominance and subordinate status in dogs overlap with behaviors used in the same way by humans (Schilder et al., 2014). Thus, van der Borg et al. (2015) identified high posture and muzzle bite as formal dominance indicators in dogs, along with low posture, passing under the head and mouth lick as submission indicators. In humans, raised posture has been noted as a dominance indicator (Mignault and Chaudhuri, 2003), along with sitting straight up (Schwartz et al., 1982) and raised head (Carney et al., 2005). Lowered head and other forms of lowered posture, such as kneeling, along with kissing, are formal markers of submission in humans (Kalma, 1991; Mignault and Chaudhuri, 2003).

Consequently, when people stroke dogs' heads, accept licks near the mouth and make themselves taller than dogs they are unconsciously expressing formal dominance over their dogs. Combined with human's total control over the resources that matter to dogs, such as food, freedom of movement, access to shelter, and even mating opportunities, this establishes dogs in a state of utter subordination to humans. Tinbergen (1969) proposed the concept of a supernormal stimulus, a stimulus that does not occur in nature but which exaggerates the features of naturally occurring stimulus and thereby evokes an exceptionally strong response. I proposed, by analogy to the supernormal stimulus, to call the relationship of human to dog "super-dominance" because no conspecific could possibly control a dog's access to resources to the extent a human does (Wynne, 2021).

The relationship of dominance offers a mechanism for dogs to respond differently to members of different species without any need to propose that dogs identify the species to which individuals belong. A dog's social behavior toward individuals from other species would depend on the extent to which the individual expresses behaviors the dog recognizes as dominant to itself along with the individual's control over resources of importance to the dog (as well as human intervention to control the dog's behavior towards a third species).

This concept of super-dominance bears no relationship to the confused notions of "dominance" espoused by certain currently popular dog trainers, such as Millan and Peltier (2007), Fincke (2004–2016), and the Monks of New Skete (2002). What these trainers mean by "dominance" is closer to concepts of positive punishment and negative reinforcement. Indeed, the "positive" trainer who controls an animal's behavior with contingent treats, strokes her dog's head and allows it to "kiss" her, is expressing dominance over her dog to a greater degree than the misguided person who imagines dominance is conveyed by always walking through a doorway first (Millan and Peltier, 2007).

This conception suggests several lines of research which may contribute to better lives for people and their dogs. For example, it is very striking that although there are now a few ethological studies of free-ranging dogs, there are almost no studies of how people and dogs live alongside each other in homes. If, as I propose, dogs' lives with people are structured around dominance relationships, dogs should react differently toward people who express different levels of dominance. Dogs would be predicted, for example, to respond differently toward people of different levels of stature, toward people with differing levels of control over resources that matter for dogs, and so forth. At present, even the most basic observational facts about how dogs and people live together are strangely absent from the literature. For example, we do not know how much time pet dogs spend in proximity to the humans in their household, what form the interaction takes nor how this depends on age, sex, breed of dog, or cultural background of the person. Consequently, the many observations that people feel affection for their dogs and the apparent reciprocation of that emotion by dogs have not been set into a context of objective measurement of behavioral interaction. Whatever the value of the super-dominance hypothesis, studies of this kind could shed light on and offer to improve dogs' lives in human society.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article and further inquiries can be directed to the author.

AUTHOR CONTRIBUTIONS

The author confirms he is the sole contributor to this work and has approved it for publication.

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REVIEW
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Working Dog Training for the Twenty-First Century

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Dogs are trained for a variety of working roles including assistance, protection, and detection work. Many canine working roles, in their modern iterations, were developed at the turn of the 20th century and training practices have since largely been passed down from trainer to trainer. In parallel, research in psychology has advanced our understanding of animal behavior, and specifically canine learning and cognition, over the last 20 years; however, this field has had little focus or practical impact on working dog training. The aims of this narrative review are to (1) orient the reader to key advances in animal behavior that we view as having important implications for working dog training, (2) highlight where such information is already implemented, and (3) indicate areas for future collaborative research bridging the gap between research and practice. Through a selective review of research on canine learning and behavior and training of working dogs, we hope to combine advances from scientists and practitioners to lead to better, more targeted, and functional research for working dogs.

Keywords: training, conditioning, detection dogs, assistance dogs, behavior, learning, working dogs

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INTRODUCTION

Dogs have long been "co-workers," collaborating with humans to complete a myriad of jobs in addition to providing companionship. Dogs have served, and currently serve, as shepherds, livestock guards, mobility assistants, therapy assistants, law enforcement canines, and supplement many more jobs. Some of the earliest reports of dogs in working roles involve assisting in hunting, dating back to at least 9,000 years ago (1, 2), as well as managing livestock and serving to some degree in wars, dating back to the times of the ancient Greeks (3, 4). Over the last 100 years, the practice of training working dogs and the science of animal behavior and training have both made significant advances. Traditionally, however, the practice and the science of animal training have developed in separate domains, with little "cross-talk" or collaborative efforts to advance both fields simultaneously. The objective of this narrative review is to briefly describe the history and scientific advances of the study of animal behavior that we view as applicable to working dog training practices, and then to identify areas for future collaborative research between researchers and practitioners to advance training practices for the twenty-first century.

Although the term "working dog" encompasses dogs that perform a wide range of functional activities, we have limited the scope of this review to three primary types of working dogs, which in present times reflect a majority of working dogs: protection/apprehension dogs, detection dogs, and assistance dogs.

The Origins: A Brief History on the Origins of Working Dog Training

Protection/Apprehension Dogs

The use of working dogs for hunting, shepherding, and for some roles in war date back to at least classical Greek times (4, 5). However, formalized training manuals and procedures did not become more common until the 20th century (6, 7), although early treatises on dog training had long been available (e.g., Xenephon's Cynegeticus). In ancient Greece, dogs' role in war is subject to debate, as either trained participants or simply placed in war, but their current duties include sentinel, tracking, protection, and detection work (4, 8). Arguably, one of the earliest and most influential training manuals for the more modern use of protection dogs is Col. Konrad Most's "Training Dogs: A Manual" published in 1910 and reprinted in 2014 (7). This text has served as the basis for military and law enforcement dog training even until present day.

Although many of the training recommendations provided by Col. Most's manual use compulsion-based methods and are outdated (see section Reinforcers and Motivation), his impacts on the field are immeasurable. Col. Most and Oscar Pfungst [the researcher that identified the Clever Hans phenomenon: (9)] teamed together in the early 20th century to conduct, what remains today, one of the most robust evaluations (and debunking) of dogs' tracking capabilities (10). Col. Most was a practitioner-scientist, conducting extensive experimental tests on dogs' tracking abilities. By developing an intricate wheel to leave shoe imprints and zip line systems to move a human after laying a track, Most experimented to identify the signatures dogs use when following tracks and found that the human was not actually necessary and dogs will readily continue to follow tracks left by a wheel device in the absence of human odor (11). This finding led Most to suggest that dogs are tracking a complex stimulus "picture," whereby the odor of damaged plants and visual stimuli also significantly contribute to the tracking performance of dogs. To a similar note, it is also worth noting that even earlier, Romanes (12) conducted an interesting series of small tests with his own dog, to elucidate that his dog successfully tracked the smell of his boots.

Detection Dogs

Training of detection dogs (narcotics and explosives) is a relatively more modern phenomenon with initial research dating back to World War II, but with wide-scale adoption occurring during the Vietnam War (3). One of the original manuals for training detection dogs was written during the Vietnam War era as part of a research program by the Southwest Research Institute in San Antonio, Texas (13). Interestingly, in contrast to more compulsion-based training procedures, this work was influenced by the developing field of Behaviorism (see section Early behaviorism) with significant influence from contemporary animal behavior research on positive reinforcement, reinforcement schedules, and minimization of aversive techniques. This manual highlights the use of schedules of reinforcement as well as controlling for and establishing food motivation.

Assistance Dogs

Assistance dog is an umbrella term that refers to a dog who is specially trained to provide support to a handler, enabling that person to live more independently by executing learned commands while also likely providing psychosocial benefits (14). Initially, most assistance dogs were guide dogs—i.e., dogs, matched with handlers who are blind, who aided in successful movement and navigation (14, 15). Over the past 45 years, the roles of assistance dogs have expanded considerably (16). For example, hearing dogs, matched with a handler who is deaf or hard of hearing, alert their handler to key sounds in the environment. Service dogs, typically matched with a person with a physical disability, perform tasks for this person that would otherwise be difficult or impossible for the person to perform (e.g., opening doors or picking up dropped items).

While depictions of dogs serving as guides for their blind handlers can be traced back centuries, the first official training school opened in Germany in 1916 (17). A little over a decade later, The Seeing Eye became the first guide dog school established in the United States. Thanks to the efforts of its initial head trainer, Eliot "Jack" Humphrey, its early breeding and training program also stood out for being extremely well-documented (18, 19). And in fact, many elements of the structure, timeline, and philosophy of the training pioneered by The Seeing Eye program remain characteristic of large schools in the guide and assistance dog industry to this day.

For example, given that so much of a guide's work transpires in public places, which always introduces a degree of unpredictability, early socialization to a wide range of environmental features is of the utmost importance. Therefore, early on, a "canine 'Head Start' program" was adopted, whereby volunteer families welcomed a puppy into their home and were responsible for the dog's early upbringing and basic obedience training [(17), p. 259]. This model is still commonly employed, with varying levels of supervision by the organization, until prospective assistance dogs reach adolescence e.g. (20, 21). It is then common for the dogs to return to a dedicated campus between 14 and 20 months, where they are housed in kennels as they progress through professional training. There is some converging evidence that the ideal age for the transition from puppy raiser home to professional training environment is around 17 months (22, 23). During professional training, dogs are taught the skills necessary for their future jobs, culminating in a multi-week joint training once matched with their new partner (17).

As part of his training philosophy, and in contrast to police dog training at the time, Humphrey was less interested in teaching compulsory obedience and was instead invested in allowing dogs to make their own decisions, even if that meant disobeying a command (17). In terms of training methods, this

mindset translated into a lack of corporal punishment, as well as a greater emphasis on the dog and handler developing a rapport, facilitated through appropriate body language and vocal tones (19). Furthermore, Humphrey felt that it was the job of the trainer to adapt to a specific dog's preferences. Because The Seeing Eye's approach differed from the standard dogma of the time, they required their instructors to essentially start from scratch, completing an intensive apprenticeship course tailored to their program and methods of choice (17). This strategy has since become a hallmark of assistance dog organizations—for example, The Seeing Eye, Guide Dogs for the Blind, and Canine Companions for Independence all require their instructors to undergo 3–4 years of specialized training, regardless of prior experience (18).

Changes Across the Twentieth Century in Animal Behavior

Like the formal documentation/manualization of animal training, the formal study of animal behavior is also relatively new. What is now known as Classical conditioning was formalized and published by Pavlov in the late nineteenth century (24), only 13 years before the publication of Col Konrad Most's original training manual, and many of the advancements in science and working dog training practice unfolded contemporaneously.

Early Behaviorism

The foundations for early behaviorism were laid by the research and work of Pavlov in the 1890s (25) and Watson in the 1920s (26). Pavlov's systematic work on learning was paramount to understanding how stimuli associated with important outcomes (such as acquiring food) can subsequently come to control and elicit a variety of behaviors when presented alone (see section How Dogs Learn*)*. This initial work, and fundamental objections to the more introspective psychology prevalent in Europe (26) led to the early behaviorist movements which focused psychology on the study of behavior rather than introspections. This opened up a range of new interest and opportunities for animal behavior research within the realm of psychology.

Another pivotal moment was the scientific re-formulation of Thorndike's Law of Effect (26, 27) into operant/instrumental conditioning, which focuses on the consequences of behavior as a modifier of the future probability of that behavior (28). This led to significant output of research on the fundamental behavior of organisms (29) investigating the effects of various reinforcement schedules (30), how stimuli can come to control behavior, generalization, discrimination (31, 32) and much more beyond the scope of this paper (33–36). Due to the focus of understanding the underlying principles of behavior, this movement led to the systematic study of model organisms, leading to advances in animal behavior. The focus, however, was understanding behavior under controlled laboratory conditions where the effects of stimuli and reinforcement histories could be easily standardized and analyzed individually. As a result, much of the research used only a few model animal species such as rodents and pigeons (29, 37), which only rarely included the domestic dog [some examples (38, 39)].

Ethology

In parallel to the development of Behaviorism—which originated primarily in Russia and the United States—the field of ethology (the scientific study of animal behavior) took root in Western Europe. In contrast to Behaviorism, ethology emphasized the importance of studying animals in natural environments, and through an evolutionary lens. Early ethologists emphasized the study of relatively innate behaviors, focusing heavily on the concept of instinct and species-specific behavioral repertoires (40). Among the key contributions of ethologists were the development of what has come to be known as Tinbergen's four questions. This framework proposes that an integrative understanding of any aspect of animal behavior requires explanation at four complementary levels of analysis, including ontogeny, proximate mechanisms, phylogenetic history, and function/adaptive value (41). The influence of this field and its perspective within the working dog field can be readily seen in trainers' focus on a dogs' "innate drive," or similar concepts such as "hunting drive" or "predatory drive" for detection dogs.

The field of cognitive ethology built on the basic principles of ethology, with emphasis on the study of animal minds in naturalistic contexts (42). Cognitive ethologists advocated for the use of field experiments, which they argued could more meaningfully probe the cognitive abilities of animals than relatively sterile laboratory tests of learning and memory (43). Cognitive ethology also brought consideration of animal consciousness to the forefront, including the challenges of understanding the minds of animals with radically different umwelts (i.e., the organism's experience of the world) than humans. Relatedly, Applied Animal Behavior (sometimes called applied ethology) emerged in the 1970s (44) in an effort to apply ethological concepts and behaviorism to issues in animal welfare and behavior. Applied animal behaviorists emphasize the importance of accommodating species-specific motivations and behavioral repertoires to improve animal welfare, often applying this knowledge to the management of captive populations. With respect to dogs, applied animal behaviorists often focus on remedying common problem behaviors such as aggression and compulsive behavior (45). Accounting for the role of the animal's immediate environment helps both in identifying the underlying cause of behavioral problems, as well as determining effective treatment and management of the behaviors moving forward. While applied animal behaviorists most commonly deal with pet populations, the same general principles can be applied to working dog populations.

Cognitive Sciences

The discipline of what is now known as cognitive science encompasses ideas and techniques from a number of related fields including psychology, computer science, philosophy, anthropology, linguistics, and neuroscience. Although many of the topics that cognitive scientists study were well-developed by the early 1900s, the formal origins of this field are often attributed to a period beginning in the 1950s termed the "cognitive revolution" (46). Thought leaders of the cognitive revolution rejected several key positions of early behaviorists, including the notion that the scientific study of psychology

should be limited to observable behavior, or that associative learning alone could account for the majority of complex cognitive processes. Rather than treating the mind as a "black box," cognitive scientists advocated for conceptualization of the mind as an information processor, analogous to those being developed by computer scientists. Like ethologists, cognitive scientists rejected the idea that minds were "blank slates," programmed largely through reinforcement history, and instead emphasized questions about innateness, modularity of mind, and species-specific cognitive processes.

Veterinary Behavior

The field of veterinary behavior is relatively new with the first board certification exam taking place in 1995, although the interest and need for clinically-oriented behavioral work was recognized and started much earlier (see https://www.dacvb.org/page/History for a brief history). The focus of this field is to bridge the gap between medical knowledge and behavioral-health issues, as well as to advance the diagnosis and treatment of severe animal behavioral issues. This growing field continues to help attend to and treat the behavioral health of working dogs (47).

Comparative Psychology

The field of comparative psychology (sometimes referred to as animal cognition) captures the intersection of the fields described above and has been heavily influenced by work in each of these areas. Thus, rather than representing a distinct field, comparative psychology describes a broad domain of research concerned with the study of animal minds, which draws on concepts from behaviorism, cognitive science, ethology, and other related disciplines.

WORKING DOG TRAINING: COMBINING RESEARCH AND PRACTICE

Canine Sensory Abilities

Before addressing how dogs learn, it is important to briefly address how dogs sense their world around them and explore the canine *umwelt*.

Visual

As a full synopsis of vision in dogs is beyond the scope of this article, we direct readers to more complete overviews of vision in dogs (48, 49). There are three main points that are particularly relevant for working dog training. First, many aspects of vision in dogs (e.g., depth perception and visual field of view, given eye placement) are highly influenced by breed (48). Second, compared to humans, dogs' visual acuity is relatively poor. Most dogs have ∼20/75 vision, meaning that dogs can distinguish something from 20 feet away that a human with typical 20/20 vision could distinguish at 75 feet away (48). Third, in contrast to humans who have trichromatic color vision, dogs have dichromatic color vision, seeing mostly on the blue-yellow color spectrum (48, 50).

Auditory

Currently we know relatively little about dogs' auditory abilities (51). However, we do know that although dogs have similar hearing ranges to humans at low frequencies, their hearing range at high frequencies is much greater than that of humans [67–44,000 Hz for dogs, compared to 31–17,600 Hz for humans; (52)]. Moreover, dogs are able to discriminate between a large number of sounds, ranging from barks (53) to human commands (54).

Olfactory

Interestingly, despite the widespread use of canines for a variety of detection tasks, canine olfactory sensitivity is poorly documented in the scientific literature. Olfactory capabilities can be roughly categorized into discrimination capabilities (ability to resolve differences between molecules or complex odor mixtures) and detection (the minimum odorant concentration required to detect an odorant).

Few studies have thoroughly explored the discrimination capabilities of the dog and how that may compare to our own sensory capabilities. From a physiological perspective, dogs are thought to have ∼1,000 different types of functional olfactory receptors (55) which is greater than the estimated 400 for humans (56) but less than the ∼1,400 estimated for rodents (55). However, how these differences in functional olfactory receptor types translate to differences in olfactory perception is not quite clear due to the complex combinatorial code of olfaction (57). Some researchers suggest humans have sufficient capability to discriminate between a trillion different odors (58), and that human olfactory discrimination capabilities are not as poor as frequently assumed (56), so the perceptual implications of dogs' increased functional olfactory receptor repertoire on their discriminatory resolution remains to be determined.

Surprisingly, dogs' detection sensitivity limits have only been measured for a handful of odorants [For a review see (59)]. Even then, differences in measures between different authors, or even different dogs within the same study, can span several 1,000 fold or more [(60), See examples of detection threshold for amyl acetate (61, 62)]. These discrepancies make broad generalizations about the canine sense of smell difficult, especially in comparison to the human sense of smell, which can sometimes compare quite poorly or even exceed the detection sensitivity of the dog (56). Despite the open scientific uncertainty on how to make generalized conclusions on canine olfactory capabilities compared to our own, evidence suggests that for many odorants, dogs can have several-fold better detection limits than our own, making them helpful partners in odor detection (59, 62).

Altogether, while much research remains to better understand canine sensory systems, the current research suggests that dogs' visual acuity is poorer than our own and may be related to breed. On the other hand, dogs' auditory sensitivity encompasses a greater range than our own. Their olfactory capabilities can also well-exceed that of humans, but it may depend on the specific odorant and how the subject is tested and evaluated. These findings do suggest, however, that for training our working dogs, auditory and olfactory cues will likely be very salient stimuli,

and dogs' perception in these domains frequently exceed our own capabilities.

How Dogs Learn: Behavioral Principles

Dogs have been demonstrated to learn though three key mechanisms: Pavlovian conditioning, Operant conditioning, and Social learning. Here we provide a brief description of each type of learning and provide a very brief review of (1) key research on the learning mechanism and (2) areas where we believe research and practice can be better studied for working dogs in the future.

Pavlovian Conditioning

Pavlovian conditioning is one of the primary mechanisms by which all animals learn. Pavlovian conditioning is a learning phenomenon in which an association between two stimuli is developed. Initially, an originally neutral stimulus comes into association via contingency and/or contiguity with a biologically relevant stimulus [such as food, water, warmth, etc. (35, 36)]. Here, the neutral stimulus becomes a conditioned stimulus (CS) as it comes to predict the biologically relevant stimulus (unconditioned stimulus; US) and the animal learns to emit a response (conditioned response; CR) when the CS is presented. The organism learns to respond to the CS even when presented in the absence of the US. The "classical" example is when repeatedly presenting the sound of a metronome immediately prior to feeding canines, the metronome (CS) alone will come to produce an anticipatory salivation response (CR) in the dogs.

Review of the Research

Although Pavlovian conditioning is one of the earliest described phenomena in the psychology literature, it remains an active area of research. A thorough review of Pavlovian conditioning is outside the scope of this paper but is covered in a variety of learning texts (34–36).

Pavlovian conditioning has several key roles in the training process for working dogs. First, Pavlovian conditioning is an important process in developing secondary reinforcers, or reinforcers that are learned through association with primary/biological reinforcers, like clickers or other secondary rewards a handler may use (63). Additionally, Pavlovian conditioning is frequently leveraged when dogs show fearful responses (64, 65), which often must be addressed with working dogs, as they are likely to encounter a wide range of frightening stimuli in their working environment but must continue to perform. Lastly, Pavlovian conditioning is a key component in detection dog training. It is frequently referred to as "odor imprinting," in which an odor is associated with a food or toy reward, although this differs from the imprinting referred to by ethologists as a specific type of learning in early life (66, 67).

Despite the importance of Pavlovian conditioning in several aspects of working dog training, relatively little research has been conducted. In the pet-dog field, several researchers have evaluated the efficacy of using a conditioned stimulus, such as a clicker during training. A recent systematic review indicates the clicker training is an effective method of training (63), but the results are less clear and often non-significant when making comparisons between training that only uses the primary reinforcer or both a conditioned and primary reinforcer (e.g., Clicker Training (68–70). However, it does appear that clicker training may lead to greater resistance to extinction (68).

The use of Pavlovian conditioning has also been evaluated for efficacy in facilitating odor detection training in dogs (71–73). Dogs that have had Pavlovian conditioning to a target odor prior to formal training learned the odor-detection task significantly faster than control dogs (72). With a follow-up within-subject design, dogs also learned to respond to a target odor to which it previously received Pavlovian conditioning faster compared to a control odor (72). Additionally, Pavlovian conditioning to odor has been shown to lead to lower detection limits for the target odor (74), and it leads to greater resistance to potential disruptors of performance such as pre-session feeding, odor distractors and extinction (73).

Translation of Research and Future Directions

Although Pavlovian conditioning is an important and critical component in odor-detection learning, it may not always be leveraged in an optimal way. Many times, in early scent detection training, a reinforcer is "paired" with a target odor to later be detected. This "pairing" or association is usually done by physically placing the two items in close proximity, such as within the same hiding box. The strength of Pavlovian conditioned response, however, is largely related to the informativeness of the CS and its relationship with the unconditioned stimulus (75). Simply pairing two items spatially does provide some spatial contiguity/similarity that can lead to associative learning, but this may not lead to the strongest behavioral response to the CS (75, 76). Further, when working with odors with low vapor pressures, which produce minimal odor availability, the potential for the target odor to be too low of salience to gain the animal's attention for conditioning should be considered in these preparations as well as the potential that other odors from the reinforcer might overshadow or block learning of the target odor [For a review see (77)]. As an alternative to spatial pairing, the reinforcer can be presented directly after the presentation of the target odor, providing temporal contiguity and contingency (if target odor is presented, then the reinforcer will follow). Interestingly, very little work has directly compared spatially pairing the target odor and reinforcer vs. presenting them in a more typical temporal preparation. In one study, dogs were trained to alert to anise extract as the target odor in a two-alternative forced choice task using two methods (78). In one method, accessible food reinforcers were available in a bin of pine shavings containing the target odor, and the comparison bin held inaccessible food but not the target odor. In the alternative method, one bin held target odor and the other did not, but the reinforcer (food) was not placed in either bin. If the dog made a response to the bin with the target odor, food was delivered immediately after (experimenter-delivered food). The results indicated that dogs learned faster with experimenter-delivered food (i.e., temporal pairing), suggesting that with the spatial food-pairing procedure may have led to food odor interference with the target odor.

Further, it could be useful to explore whether Pavlovian-conditioned reinforcers can help maintain working dog behavior when primary reinforcers, such as food and toys, are unavailable

or impractical to provide, because some research suggests conditioned stimuli can improve resistance to extinction (68). Additionally, although Pavlovian conditioning and counterconditioning are popular procedures to help address canine fears in the dog training industry, almost no research has been conducted to evaluate how these procedures could be leveraged to help prevent fear or treat working dogs that may be disqualified for minor and specific fears (e.g., gunshot fears, fear of an escalator). Although these procedures are likely broadly used in the industry, the scientific literature is largely inadequate to describe the most efficient procedure or to even generally document effectiveness of such procedures in working dog settings. Investigating and documenting successful procedures could be a fruitful area of future research, and perhaps lead to fewer canine disqualifications for fear-associated problems that might be addressed through behavioral modification.

Overall, there is a large body of research that remains to be done, applying Pavlovian conditioning to working dog populations. Specifically, we suggest that more research is needed that explores the most efficient ways to conduct initial odor-learning for odor detection dogs, the usefulness of conditioned reinforcers to maintain working dog behavior when reinforcers are unavailable, and the use of Pavlovian conditioning/counterconditioning to address fears in working dogs that may otherwise lead to their disqualification.

Operant Conditioning

Operant conditioning, also frequently referred to as instrumental learning, refers to learning due to the consequences of a behavior and is highly conserved across animal taxa (28). Behavior "operates" on the environment, leading to changes that can feed-back to the organism to change the future probability of that behavior [increasing or decreasing (28)]. This can be broken down into reinforcement (probability of future behavior increasing) or punishment (probability of future behavior decreasing). Additionally, reinforcement and punishment can be further broken down into positive and negative, referring to whether the consequence is the addition (positive) or removal (negative) of a stimulus. However, there remains debate as to whether the latter distinction (positive vs. negative) is functional and whether it should be abandoned altogether (79–81).

A thorough review of operant conditioning and its application with dogs is beyond the scope here, but many texts in learning provide thorough coverage of operant conditioning research (34–36). The focus of this review is therefore restricted to applications and questions within operant conditioning that are of particular importance for working dog behavior and performance.

Review of the Research

Discrimination Learning. A substantial number of tasks that we ask of our working dogs are discriminated behaviors under the control of some stimulus. Discrimination learning simply refers to an animal engaging in a specific behavior in the presence of a specific stimulus (and not others). Detection work provides a clear example of discrimination learning, in which an "alert" behavior is required in the presence of certain odors, but not others. However, discrimination learning also applies to all service and assistance dog tasks in which a specific behavior is expected following specified commands or in the presence of certain stimuli (e.g., navigating sidewalks, traffic lights, and crowds).

Although discrimination learning encompasses a large number of tasks that we ask of our working dogs, the methods and procedures to produce discrimination learning are typically treated as an accessory question and rarely a central focus of research. Rather, questions on discrimination accuracy/capability for various target odors or cognitive tasks have been the primary focus (82–90).

Training for Complex Discrimination Learning. Animals are able to make very subtle and complex discriminations. Dogs have been trained on complex olfactory concepts such as discriminating odors from individuals with cancer from those without [(91), e.g., (92)] or from individuals with diseases such as COVID-19 from those without (93, 94). This ability is not very surprising given the complex visual discriminations that other species have been trained on, such as natural concepts of trees vs. no trees (32), man-made vs. non man-made (95), pathology images of cancer (96), and artistic painting styles (97). These examples in other species do highlight, however, the range of complex discriminations that working dogs could potentially learn through discrimination training.

Much less research, however, has evaluated how best to train these complex discriminations. In non-canine work, research has indicated that to develop complex discriminations and concepts, it is important to train the animal with a wide range of examples/exemplars of positive stimuli (target stimuli) and negative stimuli (non-target stimuli). Thus, the size of the "set" of training exemplars is related to the animal's ability to correctly discriminate a complex concept (98–100). The same seems to be true for detection dogs learning complex olfactory concepts such as accelerants (101) and home-made explosives (102, 103), in which large numbers of training trials and examples appear necessary. However, the size of the training set and number of odor examples necessary to produce an accurate discriminated concept has not been formally evaluated in dogs.

Limited work, however, has evaluated training techniques for dogs to produce accurate discrimination of complex odor mixtures. Fischer-Tenhagen et al. (104) evaluated two methods to train dogs to identify mixtures of herbs with a target (chamomile) from mixtures without. The authors trained the dogs to either the target stimulus alone (chamomile) or to mixtures with chamomile to mixtures without. Dogs trained using either method were able to successfully respond to novel herb mixtures containing the chamomile, but dogs trained with the mixture procedure made more correct indications during the test phase. This study is similar to (102) that trained dogs to alert to ammonium nitrate and hydrogen peroxide odor mixtures. Dogs that were trained to the pure target performed poorer in generalization tests than dogs trained with odor mixtures with the target from odor mixtures without the target. Similarly, Lazarowski and Dorman (103) demonstrated that dogs struggled generalizing from detection of pure potassium chlorate to potassium chlorate mixtures unless they received training

with the potassium chlorate mixtures, further highlighting how training methodology could be an important variable influencing performance.

Errorless Learning. One potential method to facilitate complex and challenging discriminations for working dogs is errorless learning (105, 106). Under typical discrimination training procedures, the animal is free to respond to both correct and incorrect stimuli to learn that responses to correct stimuli are reinforced and responses to incorrect stimuli are not. In errorless discrimination learning, the relative salience of the correct and incorrect stimuli is manipulated at the start, such that the probability of a response to the incorrect stimulus is highly unlikely. The "incorrect" stimuli are then slowly faded in to reach a similar intensity/salience as the correct stimulus but done so at a rate that ensures the animal makes very few, if any, incorrect responses. The animal therefore learns the discrimination without making incorrect responses and is "errorless." These procedures have demonstrated robust discrimination learning in pigeons (105–107); however, the scientific literature is largely lacking examples of applying this procedure for working dogs [note see one example (93)].

Translation of Research and Future Directions

Despite the widespread use of discrimination learning by trainers for working dogs, little research has focused on how it can be optimized for efficiency in training and performance. For example, an area that holds promise for future research is the application of errorless learning for odor detection dogs. In biomedical detection programs, dogs must discriminate from complex biological samples with an undefined odor for "disease" from highly overlapping complex odor samples from patients without disease. During initial training, this task can be quite challenging for a dog; however, errorless learning procedures can be conducted by manipulating the non-target stimuli. First, dogs can be trained to respond to target odors from blank (empty) comparison samples. The similarity of the incorrect samples to the target sample can slowly be increased, by presenting diluents, until reaching comparison samples that are otherwise identical to target samples. By following this arrangement, the dog is always likely to be successful, which can help maintain motivation for the task. Importantly, however, research comparing such a procedure to a procedure in which the dog must learn through trial-and-error, and the implications each training style has for detection sensitivity and specificity, has not been conducted. Such research represents an important future direction.

Another consideration for discrimination learning is to evaluate the optimal schedules of reinforcement for training working dog tasks. During initial acquisition, continuous schedules of reinforcement are frequently used. However, for maintenance, intermittent schedules could be leveraged. Intermittent schedules are reinforcement schedules in which correct responses are reinforced following only some of the responses and could follow a variety of different schedule types (108). The benefits of intermittent schedules of reinforcement are that they lead to greater persistence in behavior if an animal cannot always be reinforced [Partial Reinforcement Effect (109–112)]. Additionally, behavior appears most resistant to disruption and extinction when high rates of reinforcement are used compared to lower rates [(113–115), For a review see (116, 117)]. Together, these results suggest that applied parametric studies that evaluate different schedules of reinforcement for working dogs engaging in their relevant task could be a useful future direction to produce the most robust behaviors in distracting environments.

Although operant conditioning is a key process by which working dogs are trained, little research has focused on how to optimize training parameters to produce the most robust behaviors in real-world and distracting environments. Such research could be fruitful translational research to optimize training programs and enhance performance. Given the basic research on procedures such as errorless discrimination, concept formation training, and schedules of reinforcement, there are several potential training methods that could be deployed and evaluated for effectiveness and efficiency in training working dogs.

Social Learning

Review of the Research

Rather than representing a single learning mechanism, social learning refers to a constellation of learning processes in which information from other social agents influences the learning process. These processes range from simple cases of "enhancement" in which an individual's attention is directed toward important stimuli or locations via other agents, to imitative capacities, in which an individual acquires novel skills by observing and modeling the actions of others. As a highly social species, various forms of social learning are likely to be important to dogs. In the last two decades, much research on dog cognition has focused specifically on processes related to social cognition, yet little of this work has been integrated into applied training protocols. Below we highlight two promising areas of research, the first exploring conspecific social learning, and the second capitalizing on dog's abilities to learn socially from humans.

Conspecific Social Learning. Altricial species (in which newborn animals are relatively immobile and highly dependent on others for survival) generally have prolonged periods of intensive contact with parents. These periods present rich opportunities for social learning and tend to coincide with key stages of brain development (118). In wolves, pups begin to accompany adults to kill sites by around 10 weeks of age yet remain highly dependent on their parents and reside in the natal pack for at least the first 10 months of life (119). It is likely that social learning, particularly from parents, plays an important role during this period. Because domestic dogs are typically provisioned by humans and are often separated from their mothers by 8 weeks of age, this may eliminate important opportunities for social learning from adult conspecifics.

To explore the potential applications of conspecific social learning in working dogs, Slabbert and Rasa (120) conducted a study in which German shepherd pups were separated from their mothers at either 6 or 12 weeks of age. The latter group was

allowed to observe the dam performing detection work between 6 and 12 weeks, presenting an opportunity for social learning. Compared to pups separated from their mother at 6 weeks of age, pups who observed the dam performing narcotics detection from 6 to 12 weeks scored significantly higher when trained and tested on this task at 6 months of age. Although the specific mechanisms of social learning were not identified, the finding suggests that social learning occurred spontaneously (dogs were not trained to attend to or mimic the actions of the dam) and facilitated subsequent training as a working dog.

Social Learning From Humans. Dogs readily learn from humans (121, 122). For instance, dogs follow human pointing from an early age [e.g., (123, 124)], and even imitate human actions in some contexts (125–127). Research investigating the "Do as I Do" method is particularly relevant for considering social learning in a training context. In this method, dogs are trained to imitate the same action that a human performs upon hearing the "Do it!" command (125–127). After a period of substantial training, dogs can learn to readily imitate human actions following the "Do it!" command, even after a 24-h delay (127).

In fact, not only do dogs readily learn from humans, but they communicate with humans as well. In particular, when dogs encounter an unsolvable (128), challenging (129), or fear-provoking task (130), they "look back" to humans and make eye contact. Importantly, though, there are differences in dogs' tendency to look back based on their training background (131–133). Most notably, highly trained dogs are less likely to look back to humans than less trained dogs (131, 133). This research highlights two important features of social learning in dogs: (1) dogs are ready to learn from humans from an early age and (2) experience, especially training experience, can influence how dogs engage with humans in a social learning context.

In fact, pet and working dogs sometimes follow human social cues even when it is not the most beneficial solution to a problem. For example, in addition to looking back to humans when confronted with an unsolvable task, dogs (pet, shelter, and free-roaming) spend almost as much time looking back at a human handler standing neutrally nearby when confronted with a novel solvable task (129, 134, 135). Likewise, studies have also demonstrated that dogs will sometimes choose to follow human gestures to an empty container, even if they can see and smell that food is located in an alternate one, and compared to non-domesticated canids, dogs persist at gazing toward humans who previously provided food or attention for much longer after human attention/responsiveness has been withdrawn (135, 136). Recently, research has identified several key genetic differences between dogs and wolves, including structural variants in the GTF2I and GTF2IRD1 genes that are associated with a hyper-social predisposition in dogs and correspond with heightened social focus on these tasks. However, genetic variation in this region has also been identified between dogs (137), and there is ample evidence that lifetime experience plays an important role in the social development of dogs (138). Therefore, it is not surprising that when dogs are given verbal and gestural encouragement to focus on an independent solution to a task, their persistence rates significantly increase and they look back to the human less frequently (129). Trained working dogs are more successful at translating this increased persistence into task success (129, 135), demonstrating that training style and history heavily influence the impact of human presence on the dog's behavior, focus, and task outcomes.

Translation of Research and Future Directions

The above research highlights how dogs are prepared to learn from social partners, but also highlights possible challenges that could occur during training or when employed in a working role. Critically, simply removing the human from the environment may not be the answer for animals used to working as part of a team, as the absence of the human partner can also lead to abnormal performance behaviors and decreased persistence (129). Especially in working roles that require the dog to engaged in independent action, the ease with which dogs may be unintentionally influenced by the actions and subtle cues of a handler or others in the environment should be considered. Prior work has shown that detection dogs can be sensitive to subtle cues and that a handler's belief about the presence of an odor can lead dogs to higher rates of false alerts (139). Additionally, more recent work has shown that handler knowledge about the number of target odors hidden can influence the length of the search and the frequency at which the dog looks back to the handler, but did not ultimately lead to differences in false alerts (140). These results suggest dogs' sensitivity to human action can be both a help and a hindrance; however, greater awareness of human influence can help shape practices that better control for unwanted influence and utilize dog's acute awareness of social stimuli to the working team's advantage.

To our knowledge, the explicit application of social learning in working dog programs remains relatively rare. However, we propose several ways in which research on social learning may pertain to working dog training programs. With respect to conspecific social learning, working dogs are commonly separated from their litters by 8 weeks of age, limiting opportunities for social learning that might be more common in the socioecology of feral dogs or their evolutionary forebears. Thus, waiting to separate dog pups from their mother and allowing dog pups to observe their mother performing tasks until 12 weeks of age might lead to enhanced training outcomes. Alternatively, if delaying transition to foster homes leads to fewer exposures and experiences outside of the whelping and kennel environment for the puppies, this recommendation may be contraindicated and lead to more fear, highlighting the need for more research to establish best practices.

In addition to this early-life social learning, there are other important opportunities for conspecific social learning that can be fostered (and experimentally evaluated) in adult working dogs. For example, many working dogs are trained at dedicated facilities in which individual dogs alternate between bouts of active training with a human handler, and periods of rest and downtime while the trainer works with other dogs. These periods of downtime, however, may present opportunities for social learning, especially if dogs have opportunities to observe other dogs actively being trained. The potential utility of this approach could easily be evaluated using experimental designs in which

some dogs are given rest and downtime in isolation whereas others are given opportunities to observe other dogs in training during these periods.

Assistance dogs, detection dogs and search-and-rescue dogs frequently need to be habituated to potentially fear-provoking scenarios such as navigating large crowds, navigating escalators, walking over rubble or being exposed to gunfire. Frequently, dogs are habituated or desensitized to these conditions individually. Social learning literature suggests there may be benefits to a dog first observing a conspecific navigating these scenarios comfortably and confidently. However, such experimental research has not yet been done, and so would be interesting and useful to conduct in the future.

Additionally, with respect to social learning from humans, dogs can be trained to imitate human actions using the Do-as-I-Do training program. This training program allows more flexibility in the types of actions that dogs can learn to perform as they simply imitate whatever action the human performs and can retain this information even after a considerable delay. Notably, incorporating Do-as-I-Do involves a substantial initial investment in training the "imitate" command, but may pay dividends if it can be subsequently used to rapidly train a variety of other behaviors. Thus, we expect this approach may be particularly useful for dogs required to master large repertoires of trained behaviors (e.g., service dogs) more so than dogs who are trained to perform a smaller set of commands. Notably, once established, Do-as-I-Do training has been shown to facilitate faster skill acquisition than traditional operant techniques, and is associated with more robust transfer of trained behaviors to novel contexts (126).

Reinforcers and Motivation

Review of the Research

A combination of evolutionary, genetic, developmental, and lifetime factors may influence the salience of specific stimuli to an individual, breed group or to dogs in general. This is true for both perception and responsiveness to stimuli that precede a behavior (such as releasers or discriminative stimuli) and stimuli that follow/act as a consequence for the behavior, including reinforcers and punishers. For example, breeds of dogs traditionally selected for a strong motivation to chase (e.g., Border Collies or German Shepherd dogs) may be predisposed toward greater responsiveness to a variety of moving stimuli compared with dogs from breeds selected for inhibition of these traits, or a higher response threshold to moving stimuli, such as Anatolian Shepherd dogs and Great Pyrenees (141). Genetic differences associated with attentional bias toward social stimuli have similarly been found to correspond with assistance dog success (137). When the working role of a dog requires behaviors that are associated with motor patterns that have biological relevance, or motor patterns that have been selected for within a specific working breed, the motivation for engaging in the behavior may be intrinsic and require less shaping and external reinforcement than when dogs are being trained to display behaviors or do jobs that are less related to their natural behavioral repertoire. Therefore considering the domestic dogs behavioral ecology, as well as motor patterns and biological predispositions under selection when breeding working dogs, may inform what jobs dogs will do best, and inform training practices in ways that allow handlers to utilize a dog's predispositions and motivations to aid the training process (142).

Socialization and lifetime experience are also known to greatly influence how dogs perceive and interact with stimuli in their environment and can also contribute to motivational factors (138). Other motivational factors, including what establishing operations (i.e., environmental circumstances that make a behavior more or less likely) may best set the stage for effective training or job performance, are also important to consider. For example, factors such as the timing and duration of the training session, degree of hunger or thirst, temperature, time since last entering the training area, or interacting with the trainer, and many other factors can influence motivational state and therefore a dog's inclination to focus and persist on training tasks. Furthermore, considering how environment and motivational factors may differ between a training environment and final work setting can be used to simulate final working conditions or highlight the importance of training sessions in applied settings. Likewise, not all dogs (even within the same breed or training program) will find the same items or activities as reinforcing as others (143). In fact, what some dogs find reinforcing, others may find aversive, or frightening (144). Additionally, the same dog may not find the same items or activities reinforcing or aversive all of the time.

Dogs may also differ in degree of persistence Rao et al. (145), inhibition (129, 146), or baseline arousal levels (147), which in turn may influence what reinforcement schedule is optimal. Because of this variability, it is not possible to describe the ideal motivational considerations and reinforcers for all working dogs here, although there is a great need for more research looking at the efficacy of training practices, including managing establishing operations and reinforcers, across a wide range of working settings. However, several concepts well-studied in the literature across a broad range of species (including dogs) may serve as a scientific basis for deciding what motivational and reinforcement strategies could work best for individuals or groups of dogs within a specific training context.

Translation of Research and Future Directions

Preference Assessments. Identifying the high-valued reinforcers is critical for a successful training program. Frequently, dogs are selected based on whether a certain reinforcer is highly motivating for a dog (i.e., "ball drive" or "toy drive") through a variety of selection tests (148). An alternative concept that may help prevent the failure rate of dog training programs is to provide preference assessments that allow the trainer to select highly motivating reinforcers for the dog, rather than selecting a dog for the reinforcer. For example, potential working dogs could be evaluated for motivation for a variety of food, social, and toy rewards to create a hierarchy of reinforcers that could be used. The methods of preference assessments themselves are generally well-established (143, 149–151), making this strategy straightforward to implement. Additionally, by establishing a range of potential reinforcers, issues associated with satiating one reinforcer may be prevented by having alternatively available

reinforcers. Further, this strategy would also allow for a range of studies investigating whether reinforcement schedules that provide varying reinforcer types may lead to more persistent behavior less susceptible to satiation.

Establishing Operations. Maintaining and controlling reinforcer value is important to preserve any trained behavior. However, how best to do so for working dogs has not been previously researched and would be a useful future direction. Various agencies have practices to help establish their reinforcers as high value, such as only allowing the dog access to the reinforcer during training, whether it be a certain type of toy or food. However, it is not clear whether these more extreme schedules are necessary to establish the desired behavior. It is possible that selecting dogs with a "high drive" for a particular reinforcer and only providing access through irregular training may lead to the development of alternative or undesired behaviors. For example, high levels of motivation produced through deprivation can lead to higher levels of generalization (152), which could produce new behaviors or responses to non-target odors that are undesirable. Further, in many working dog applications, much emphasis is placed on selecting dogs with extreme motivations for reinforcers such as toys. It is unclear, however, whether ultimate performance as a working dog is linearly related to reinforcer motivation (i.e., more "drive" leads to better performance). Alternatively, there may be an inverted-U function for some tasks that require attentiveness, in which there is an optimal level of motivation for the reinforcer and very low or very high levels of motivation may each produce performance decrements. Thus, future research manipulating establishing operations and its impact on working dog performance may be a useful future direction to optimize consistent performance and motivation.

Use of Aversives. Incidental effects from the use of aversives have been documented in the basic research literature, such as elicited conspecific aggression (153), fear of punishment associated stimuli (154), and substantial suppression of all behavior within a punishment context (39, 154, 155). Growing applied literature with dogs highlights that positive reinforcement based training is effective and the use of aversives can have negative welfare side effects for the dog (156–161). This highlights the need to further consider not only how to motivate working dog behavior (e.g., does the dog engage in the behavior to receive a reward or to avoid a correction), but also which methods produce the best performance *and* welfare outcomes for working dogs. In this respect, treating our working dogs as "student learners" and evaluating how to arrange environmental conditions that set working dogs up for success may promote successful performance and welfare outcomes.

How Dogs Think Can Inform our Training

Review of the Research

A full overview of research on how dogs think is outside the scope of this article. For a more comprehensive overview see Bensky et al. (162). At the broadest level, there is a growing body of work on how dogs think about both the social and physical world. We cover each of these domains of canine cognition in the sections that follow.

Social Cognition: Thinking About the (Human) Social World. Given that the majority of research on social cognition in dogs has explored how dogs think about humans, we will limit this review to what dogs think about the human social world. These findings are of relevance to working dogs because they highlight ways in which working dogs may work with, learn from, and understand their trainers.

Perhaps most notably, dogs have some aspects of a "Theory of Mind" and are able to make inferences about some human mental states (163). In particular, dogs are able to interpret a human's visual perspective [i.e., understand what a human can see (164, 165)] and they also seem to expect that humans will remember what they have seen [i.e., have knowledge of what they have seen (166–168)]. Moreover, dogs respond to human intentions and can identify when a human intends to communicate with them (169) and when humans are performing goal-directed actions (170). In addition to evaluating human mental states, dogs respond to human emotional states (130, 171, 172). For instance, dogs will fetch an object that a human has emoted positively toward in the past (172) and are more likely to go toward a scary object if their owner has emoted positively toward it (130). Further, some work suggests that training may impact a dog's tendency to react to a person's emotional state. In particular, in one study, dogs trained for water rescue were less likely than pet dogs to approach a novel object simply because a person had emoted positively toward it (173).

Building on dogs' understanding of human emotional states, dogs, in some cases (but not all), will help humans when they are in emotional distress and in need of help (174–177). Interestingly, work so far suggests that this tendency to help is not influenced by therapy training, as therapy dogs in one study were no more likely to help than non-therapy dogs (176), though more work is needed to explore the influence of other types of training. Furthermore, dogs will not only help humans in times of distress, but they will also cooperate with humans on joint goals (178). Interestingly, though, dogs struggle to spontaneously cooperate with one another (179).

In addition to understanding something about human mental states and emotions, there is evidence that dogs can evaluate humans based on who has recently been "nice" or "mean" in some contexts (146, 180–182). However, this ability may be limited only to those dogs who receive certain types of training. One recent study suggests that only agility trained dogs, not pet dogs, showed a preference for a helpful experimenter over a hindering experimenter (183).

Finally, there is growing evidence that dogs have some understanding of human language (184, 185). Not only are dogs able to learn the names for many objects, they can learn new words via a system of "fast mapping" wherein they learn the names of new objects via a process of exclusion (184). Specifically, if they know the name of three objects, and someone requests a novel word (e.g., "blicket"), dogs are capable of inferring that the fourth object they do not know the name of must be "blicket." Building on this, there is some evidence that dogs are capable

of understanding language syntax (185). However, it should be noted that this work has been done with a handful of highly trained dogs, so it is unclear to what extent these findings generalize to other dogs.

Thus, in at least some cases, dogs understand human intent and emotions, provide help to humans when they are emotionally distressed, cooperate with humans, prefer humans who are "nice" over those who are "mean," and show some comprehension of human language. Taken together, these findings have the potential to impact working dog training because they highlight ways in which working dogs may relate to their trainers, understand their trainers' behavior, and language.

Non-social Cognition: Thinking About the Physical World. Understanding how dogs think about the physical world is crucial for supporting best practices in working dog training because it gives us insight into the ways dogs think about and see the world. Through understanding dogs' cognition, we can determine which training practices interface best with their understanding of the physical world.

Dogs understand many of the same features of the world that human infants do. For instance, they have a basic understanding of object solidity [i.e., that objects are solid and other objects cannot pass through them (186)] and object permanence [i.e., that when objects are out of view they continue to exist; e.g., (187)].

Building on this, dogs seem to have at least a basic sense of number and quantity. They can distinguish between large quantities (e.g., 10 pieces of food or greater) and small quantities [e.g., 5 pieces of food or fewer (188, 189)], and in some cases can discriminate between small numbers under 5 [e.g., tell the difference between 1 and 2 (190)]. However, dogs' ability to discern objects based on number may be context-specific because they do not demonstrate this ability in every experimental context (191).

Another crucial aspect of non-social cognition is memory. Dogs seem to have a working memory capacity of a few minutes. Research has shown they are able to keep the location of hidden objects in working memory for up to 4 min (192). However, the duration of dogs' working memory, and other executive functions, decline with age (193, 194). In addition to working memory, some recent work suggests that dogs may be capable of the elements of episodic memory (195), including the what, when, and where of odor cues (196). Further, dogs' working memory for odors can be quite expansive, with recent research indicating dogs' odor working memory in an odor span task is upwards of 72 odors, which is similar to rats (197, 198). In terms of long-term odor-memory, dogs are able to readily learn to detect 10 different target odors successfully, but the experiment did not evaluate beyond 10 odors (199). Interestingly, little work has evaluated retention of odor memory in dogs, but a small study of three dogs found dogs maintained accurate odor discrimination performance after a 69 day delay (200). Most recently, extending these results Lazarowski et al. (201) found dogs' memory for odor recognition to remain largely robust over 12 months with minimal training. These parameters are critical for further exploration given that typical odor detection dogs are frequently trained to more than 10 target odorants, and it's unclear the necessary interval for "refresher" training to maintain optimal performance. Dogs are frequently given weekly training, but this may be unnecessary given the results of Lubow et al. (199) and Lazarowski et al. (201) but more extensive work is necessary before best practices can be established.

Recently, researchers have begun exploring the contextual factors that affect dogs' ability to remember learned tasks. Preliminary research suggests that engaging a dog in activities that likely induce "pleasant arousal," such as walking and play, directly after learning a new task has positive effects on their memory for that task when tested again 24 h (202), 1 week (203), or even up to 1 year (204) later. In contrast, having them immediately engage in learning of an unrelated task results in cognitive interference, thereby disrupting memory consolidation (203). Interference in memory tasks also seems to be critical for odor memory in dogs (205). Sleep appears to be another crucial variable (206). In dogs specifically, performance in learning new commands has been shown to be enhanced by sleep-related improvement in memory consolidation (203, 207, 208). Given that command learning is an integral part of working dog training, these findings, along with an emerging literature on the environmental factors that affect quality and quantity of sleep (209), are of great relevance. For example, these findings can inform how trainers structure the duration and timing of their training sessions with regards to other activities, especially when teaching new commands. Perhaps shorter sessions over multiple days, separated by more opportunities for play and sleep, would pay greater dividends than packing multiple sessions into a single day.

One domain of non-social cognition where pet dogs do not excel is independent problem-solving. Compared to wolves and dingoes, pet dogs often struggle to figure out how to solve puzzles based on causal reasoning (210–212), and when dogs do figure out how to solve problems at the group level, there is often significant variation at the individual level (213). Given that pet dogs are less adept at solving physical problems than non-domesticated canids and demonstrate large individual variation in problem-solving abilities, some scholars have suggested that artificial selection may have relaxed selection pressures for independent problem solving (210). That said, training appears to impact dogs' propensity to solve problems, as highly trained dogs are more adept at solving physical problems than less trained dogs (131, 133). It remains unclear, however, whether this is a byproduct of training that enhances problem solving or rather reflects that dogs with enhanced physical problem solving are more receptive to advanced training.

Overall, when it comes to dogs' understanding of the non-social world, they have a basic understanding of object properties, some understanding of quantity and number, and a working memory capacity of a few minutes. That said, dogs are not naturally adept at individual problem solving, though training seems to enhance their ability. Taken together, these findings have the potential to impact working dog training because they highlight both strengths and weaknesses of dogs' cognition that may impact which training methods are most tractable.

Translation of Research and Future Directions

Although a growing body of work investigates the impact training can have on canine cognition [e.g., (131, 133, 173, 183)], no empirical work to our knowledge has yet integrated basic research on canine cognition with research exploring the effectiveness of various training methods. It is our hope that the brief review of canine cognition above will stimulate ideas regarding how to translate this basic research into effective training methods. However, a few findings in canine cognition are of note for trainers. First, it may be useful to keep in mind the areas in which dogs excel. Dogs track human emotional states [e.g., happiness, anger, disgust; e.g., (130, 171, 172)], and in some cases even their mental states [e.g., knowledge, goals; e.g., (167, 170, 214)]. This ability suggests that training involving these social cues may be effective. Additionally, research evaluating how sleep or engaging in enjoyable activities following training may facilitate memory and later performance could be of particular importance to enhance training success.

Likewise, it is important to keep dogs' cognitive limitations in mind in a training context. Notably, in the absence of formal training, dogs do not naturally excel at independent problem solving [e.g., (210–212)]. Thus, training methods that rely on dogs' individual problem-solving skills may prove less effective than other training methods. Moreover, although dogs do have a sense of number, this can be context-dependent and dogs do not demonstrate this understanding in all contexts e.g. (190), indicating that planning training situations that require dogs to make these discriminations would not be as effective or efficient.

Human-Animal Bond

Review of the Research

While there are multiple factors that may be important when considering how the human-dog relationship can influence working dog performance, there is growing evidence that the success and well-being of both the human and dog involved in a working partnership can be significantly impacted by the quality of bond shared between the two. Even in adulthood, dogs have been shown to form attachment bonds with humans that resemble conspecific infant-caregiver attachment relationships (215). While dogs can form bonds with new humans quickly (216), the quality of these relationships can vary, with some environments and experiences resulting in higher rates of secure attachment bonds than others (216–218).

Secure attachment refers to a persisting relationship between two individuals (in this case a dog and a human owner, handler, or trainer) that promotes proximity seeking, contact exploration balance, and stress reduction in unfamiliar environments or situations (219). While attachment is the product of a mutual bidirectional relationship, it can be assessed from both the perspective of the human (through behavioral evaluation or surveys) and the dog (through behavioral evaluation).

While the recognition that dogs and humans can share deep bonds is not new, research investigating the quality of these bonds from the dog's perspective has been limited. Only recently have scientists begun to ask about different styles of attachment that dogs show toward their caretakers, or the impact of attachment security (or insecurity) on the dog's behavior and welfare (217, 220, 221). While even less research has been done specifically on working dog attachment relationships, the quality of owner/handler bonds may be an important factor in training and job success. In fact, one study found that working search-and-rescue dogs were more likely to have secure attachments to their human partner when compared to pet dogs [although this difference was not statistically significant (219)]. If further research finds such trends are representative of a true population difference, it will be important to understand why. For example, an enhanced bond could be due to the influence of working dog training, or simply additional time spent with the human, on attachment quality, or conversely it could suggest that dogs with secure attachments are more likely to be successful working dogs. Additionally, secure attachments are, by definition, relationships that reduce stress, especially in novel, or unfamiliar contexts (222). Focusing on attachment or other aspects of relationship quality between dogs and their trainer(s), owner(s), and handler(s) may therefore be valuable in terms of sustainable and humane practices independent of whether the bond improves other aspects of training success (221, 223).

Translational Research and Future Directions

For many working dogs, training and/or work will require living in multiple places, as well as frequently working in new environments and/or with new people (224). While some trainers, fosters, or other short-term caretakers express concerns about developing a strong bond with dogs in their care temporarily- often for fear that breaking the bond will harm the dog when they are rehomed (225)- research to date suggests that forming a secure bond may instead have an important and positive impact on the dog's success and well-being in both that environment and the next. The broader literature has demonstrated that even when dogs transfer handlers, high quality secure attachments developed earlier in an individual's life can be beneficial and predictive of the formation of new secure attachments at later stages of life for both humans (226, 227) and dogs (223). Considering the other side of the relationship, evidence to date indicates that dogs with secure attachments to their human caregiver are on average more persistent, more exploratory and also show fewer behavioral signs of stress and neuroticism in novel environments (217, 220, 228). The quality of attachment that humans report sharing with their own dog, or a working dog partner, has also been found to be predictive of therapeutic benefits and/or the beneficial impact of that dog on the human's quality of life (218, 229, 230).

While a relatively new area of study, there is already some evidence that the attachment style of working dogs toward their caretaker or handler may be an important aspect of training success and job performance. Differences in focus or comfort level in novel situations, associated with the presence or absence of a secure base effect, could potentially impact training, or performance (224). For example, one study found that trained therapy dogs were able to perform the function of remaining near a mock therapy participant equally well, independent of their attachment style toward their handler. However, dogs with insecure attachments spent more time looking back at their

handler (and away from the therapy participant) during the session (224). Such behavioral differences could be meaningful, as looking away may signal discomfort on the part of the dog and could also be interpreted as disinterest by the human therapy participant—which could reduce therapeutic success. However, more research is needed to better understand the impact of such outcomes. Dogs with secure attachments to human caretakers/handlers have also been found to show greater task persistence (217) and increased readiness to engage in object manipulation (228), traits often relevant to working dog training success. Given that, in humans, attachment style has been used to predict a wide range of factors related to executive functioning (231), learning success (232), and career success (233), more research into the ways that dog-human attachment relationships may impact a working dog's training and performance is needed.

FORMALIZING HANDLER EXPERTISE

In this review, we have identified several directions and needs for formal research with working dogs, thereby providing an important basis to move research in new directions. However, it is also critical to note the vast body of animal behavior knowledge that expert trainers have developed through daily experience. Much of this knowledge is unpublished, not widely available, and rarely appears in the scientific literature, even though it may have been developed over decades of informal testing. To fully move the field forward in a collaborative way, systematic research through expert interview and qualitative research methods could be a highly beneficial practice to formalize some of the procedures, thought processes, and experience developed by expert working dog trainers e.g. (234). Although expert trainers may not have a scientific explanation or justification for their observations or procedures, finding a way to formalize their years of hands-on experience and feedback (via dog performance) could yield a wealth of information that would save researchers valuable time and resources. It is important that practices are ultimately held up to an empirical evaluation, so formally documenting the lessons learned by expert trainers would be an important step forward to generate collaborative work that builds upon trainer expertise (rather than re-developing it), addressing the most critical questions important to both the researcher and trainer.

CONCLUDING REMARKS

Working dogs are trained to complete a myriad of tasks for service, assistance, detection, and protection work with much success. And yet not all working dogs that enter training programs are successful (235), leading to high costs and limited availability of working dogs. Optimizing training efficiency represents one way to increase the probability that a dog will be successful. Over the last 100 years, our scientific understanding of animal behavior has grown and expanded rapidly and so has the expertise and methods of training working dogs. It is our hope that this review inspires new directions of collaborative research between researchers and working dog practitioners with the goal of expanding evidence-based information and techniques that future working dog trainers can incorporate. The synergy of these two areas will likely result in improved training practices and have a measurable impact on the outcomes, welfare, and availability of working dogs filling needed roles in our society.

AUTHOR CONTRIBUTIONS

All authors contributed to conceptualization, investigation, funding acquisition, writing–original draft, and writing–review and editing. In addition, NH contributed to supervision.

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REVIEW
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Advancing Genetic Selection and Behavioral Genomics of Working Dogs Through Collaborative Science

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The ancient partnership between people and dogs is struggling to meet modern day needs, with demand exceeding our capacity to safely breed high-performing and healthy dogs. New statistical genetic approaches and genomic technology have the potential to revolutionize dog breeding, by transitioning from problematic phenotypic selection to methods that can preserve genetic diversity while increasing the proportion of successful dogs. To fully utilize this technology will require ultra large datasets, with hundreds of thousands of dogs. Today, dog breeders struggle to apply even the tools available now, stymied by the need for sophisticated data storage infrastructure and expertise in statistical genetics. Here, we review recent advances in animal breeding, and how a new approach to dog breeding would address the needs of working dog breeders today while also providing them with a path to realizing the next generation of technology. We provide a step-by-step guide for dog breeders to start implementing estimated breeding value selection in their programs now, and we describe how genotyping and DNA sequencing data, as it becomes more widely available, can be integrated into this approach. Finally, we call for data sharing among dog breeding programs as a path to achieving a future that can benefit all dogs, and their human partners too.

Keywords: dog breeding, genetic selection, behavior, genomics, heritability, EBV, working dog, guide dog

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INTRODUCTION

A successful working dog is healthy, physically fit, and able to perform at an exceptionally high-level, with the behavioral, physiological, and structural characteristics required varying by job (1) (**Figure 1**). Over the past 20 years, especially since the attacks of September 11, 2001, the demand for high-quality working dogs around the world has soared, while the supply of these dogs has either remained unchanged or declined, resulting in increasing costs even as the quality of the dogs has suffered (2–4). With rates of visual impairment and blindness in the United States anticipated to double by 2050 as populations age, requests for guide dogs, already often difficult to access (5), will almost certainly increase further (6). To meet this increasing demand, organizations that breed working dogs need to use scientifically proven, modern breeding best practices that can increase the production of high-performing, healthy dogs (7).

FIGURE 1 | Skills required of a high-performing guide dog. A high performing working dog is required to fulfill a demanding set of criteria that vary by working dog type. While some, such as resilience, are required for nearly all working dogs, other skills are job-specific. To illustrate this, we describe some of the major requirements for a guide dog, the working dog type bred by Guiding Eyes for the Blind. **(A)** A guide dog must not be frightened of or bark at things that typically alarm other dogs. When working, they must ignore distractions such as other dogs or other animals around them. **(B)** They must be comfortable leading out with a steady pace and pull when working in harness, while also remaining calm and focused in all situations. They must learn a wide range of commands, but also be able to ignore commands when they are not safe, and problem-solve when a command is not possible. **(C)** When there are obstacles or dangers in the handler's path, a guide dog must alert the handler by stopping, or navigating their handler around the obstacles, and then resume walking in the target direction. When working, they should not be distracted by other people. **(D)** A guide dog must resist chasing things while working, and ignore enticing scents, including food. **(E)** A guide dog needs to be physically healthy, and matched to the stride and personality of their handler. Image credit: Kathleen Morrill.

Working dogs, in various forms and with various functions, have been part of human societies for thousands of years. Sled dogs were used in Eastern Siberia over 9,000 years ago (8, 9), and ancient Romans had both livestock guarding dogs and hunting dogs (10, 11). During this time, humans likely exerted ***postzygotic selection*** by favoring the highest performing dogs, increasing the prevalence of desirable traits among their offspring. Compared to modern dog breeds, ancient working dog populations were outbred and genetically diverse. Modern dog breeding started in the mid 1800s, and historical records and genomic studies suggest modern dog breeders predominantly favored form and pedigree over function (12, 13). The genomic loci most differentiated between breeds have been implicated in physical traits like body size, coat characteristics, and ear shape. While all dogs in a modern dog breed may look similar to one another, behavior and personality is highly variable.

Because the genetic variants that confer working dog traits predate modern breeds, any dog, purebred or not, may, by chance, inherit the genetic profile of a high-performing working dog, although this probability may vary depending on the dog's breed ancestry. The goal of selective breeding is to increase the average ***genetic merit*** of a population, thereby increasing the likelihood that, in the next generation, more dogs will be higher-performing than dogs in the current generation. To reach this goal, successful breeding programs will also attempt to optimize the environment in early puppyhood for long-term success (14–17).

Implementing a successful working dog breeding program is enormously challenging because of the complexity of the traits themselves, and the risk of inbreeding and other inadvertent consequences. Behavioral traits, difficult to breed for because of their genetic complexity and environmental malleability, may also be the most critical (18, 19). If not done with care, selective breeding can significantly reduce genetic diversity of the population, leading to increased rates of disease and shortening lifespans (20). While using dogs from outside populations as breeders can restore diversity, it risks lowering the success rate of the importing breeding program for generations, if the imported breeder is of lower genetic merit. Even successful selection programs can have unexpected consequences. Selection for dogs that are easy to control, for example, may increase the rate of excessive body sensitivity.

To address the increasing demand for working dogs, canine breeding programs need to utilize modern animal breeding practices, including cutting-edge, and rapidly advancing, genomic technologies. Here, we provide a roadmap for implementing a modern canine breeding program, and describe the synergistic collaboration between two non-profit projects to support dog breeders transitioning from time-worn techniques to modern, scientifically proven methods. The ***International Working Dog Registry (IWDR)*** is a centralized database that already contains uniformly coded records on over 64,000 dogs. Uniformity in coding is accomplished using drop-down lists of coding choices, from which one must be chosen, with very little free-text permitted anywhere in a dog's record. IWDR implements modern animal breeding tools within the registry, and it supports training for breeders seeking to employ genetic selection. The ***Working Dog Project*** is an open-science initiative for working dog genomics, designed to engage tens of thousands of dogs in research studies to develop the next generation of

genomic and medical technology for dogs. Working together, the two aim to increase the supply of high-quality working dogs, while supporting research to improve the health and welfare of all dogs.

BREEDING WORKING DOGS

Managers of working dog breeding programs face the daunting challenge of producing large numbers of puppies, often over 100 per year, while maintaining, or even increasing, the percentage of successful dogs. There is almost always at least one plausible reason not to breed a young female, or to avoid a particular mate, especially when the goal is to avoid producing any disease-affected puppies, but this has to be balanced against the need to produce puppies that easily develop into behaviorally appropriate adult dogs. To balance these competing forces, a production plan needs to be followed that includes an objective method for choosing young dogs to become parents of the next generation. By following this plan, selection will change allele frequencies in the population, and the puppies produced in each successive generation will be healthier and endowed with more desirable behaviors than those of their parents. This objective, science-driven approach, proven to work by large guide dog breeding programs (7), has clear advantages over today's most common approaches to dog breeding.

At conception, each future puppy inherits its genetic foundation (***genotype***) from its parents. The local environment in which each genotype develops into a working adult has the potential to mold and shape that genotype in a myriad of ways. The ultimate challenge of dog breeding is to wisely use observed ***phenotypes*** to accurately predict the non-observable underlying genotypes.

For centuries, dog breeders have used ***phenotypic selection*** to influence observable traits or behaviors seen in a population. This traditional process, where dogs are chosen to become parents based on their individual phenotypes, has slowly molded and shaped ancestral dogs into today's modern breeds (21, 22). Using this process to produce genetic change, however, is very challenging because a dog's own phenotype is often a rather poor predictor of the dog's true genetic merit or genotype. Scientifically advanced working dog breeding programs of today utilize a data-driven method called ***estimated breeding values (EBVs)*** for meeting this challenge. It incorporates statistics and phenotypes to more accurately identify young dogs to be kept for breeding, even before producing their first litter.

Just as in phenotypic selection, EBVs rely on trait measurements made on individual dogs, but the calculation process is objective, deterministic, and grounded in modern statistical prediction theory. Furthermore, many people can learn how to use EBVs, even if they do not fully understand the process by which EBVs are calculated. For molecular geneticists, it may be helpful to know that EBVs in the context of this paper are very similar in concept to ***polygenic risk scores*** in human genetics (23), but with one fundamental difference. In the animal breeding world, the family structure of most populations includes rather large half-sib and full-sib families. The process for producing EBVs takes this family pedigree structure into account.

Since the 1940s, livestock breeders have used some form of EBVs and genetic selection to obtain genetic change in economically important production traits (24, 25). For example, breeders of American Angus cattle increased average weaning weight of bull calves by about 4 pounds per year between 1972 and 2021 (26). Similarly, between 2000 and 2016, US dairy cattle breeders, by applying selection pressure to increase the productive life, achieved an increase of about 10 months (27). Using exactly the same techniques as the livestock breeders, the dog breeding program at The Seeing Eye improved trainability for working as a guide while reducing the frequency of phenotypes that impact working longevity, including poor hip quality (7). After eight generations of selection, the percentage of dogs with an excellent hip quality score (as assessed by an extended view hip score) increased from 34 to 93% in German Shepherd Dogs and from 43 to 94% in Labrador retrievers.

Phenotype selection, when carefully implemented, can be effective for altering the prevalence of single traits. In Sweden, phenotype selection alone reduced rates of moderate to severe hip dysplasia in at-risk breeds by one third (28). However, genetic selection results in more improvement than phenotype selection (29), allows for continuing improvement even after phenotype selection has reduced the frequency of undesirable characteristics, and makes it possible to select on multiple traits in parallel (28).

The advent of inexpensive whole-genome genotyping and sequencing technology could allow relative genetic merit to be predicted more accurately from genotype in the future (23). These powerful approaches are not yet possible, but offer the potential to further improve on EBV selection.

BEST PRACTICES FOR GENETIC IMPROVEMENT IN A BREEDING POPULATION

Working dog programs and breeders using only phenotype selection will find it difficult, if not impossible, to maintain and improve the health and performance of their dogs over many generations. The vast majority of traits are complex, with tens or hundreds of different genes shaping a dog's inherited genetic potential, which is further influenced by their environment. To increase the frequency of a phenotype in a population, dogs should be selected for breeding based on the likelihood that their progeny will exhibit that phenotype. While adult phenotype is a reasonable proxy for this likelihood for a simple genetic trait, like coat color or hair type, for ***complex traits*** (e.g., behavior, or susceptibility to diseases like cancer) the correlation is much less clear.

Using phenotype selection, genetic improvement will be, at best, slow. Selecting dogs for breeding based solely on their adult phenotype is an inefficient way to increase the frequency of polygenically inherited desired traits in the next generation and is likely to lead to reduced genetic diversity and increased rates of disease (20, 30, 31). Breeders will often invest significant

time and resources in attempting to identify genetically superior dogs by studying pedigree databases for evidence of the desired trait in related dogs, but this approach lacks a systematic means of ranking an individual's genetic merit based on its family relationships.

EBV selection is far more powerful than phenotype selection. The EBV for a given trait on a specific dog is calculated using phenotype data, both from that dog and from all related dogs in the population, when those data are available. Because most breeding plans are focused on improving more than one trait, each dog will have a set of EBVs, one for each trait. This set of EBVs for multiple traits can then be combined into one overall ***selection index*** that weights each trait based on its importance to the breeding program (32–34). This overall selection index value then reflects each young dog's overall relative genetic merit, which is also an indication of the dog's ability to produce offspring with all the phenotypes included in the breeding goal. By using an overall selection index, breeding program managers can identify a genetically diverse cohort of young dogs most likely to confer desired traits in their offspring.

Despite its utility, EBV selection has not been widely used in dog breeding because it requires large, accurate pedigrees and phenotypes assembled into one uniformly coded database, as well as expertise in statistical genetics and data processing. These requirements have hindered adoption of EBVs by smaller breeding programs, and programs without access to the required expertise. To address this need, IWDR includes EBV calculation and data management tools that are accessible to all dog breeders. Through the IWDR database, breeders can obtain EBVs, allowing them to objectively identify which young dogs are most likely to produce puppies that move the population's average phenotypic merit closer to the breeding goals defined by the breeding manager.

SIX STEP APPROACH TO EBV SELECTION

Implementing an EBV-based selection program can be daunting. Here, we distill the process into six steps (**Figure 2**). Using this approach, breeding programs can systematically apply the scientific principles of population genetics and genetic selection to their dog populations.

Step 1. Define the Goal(s) of Selection

Before applying any selection in a breeding program, it is critical to establish clear goals, such as improving success rates. With the goals defined, the program can then identify measurable phenotypic traits relevant to achieving those goals.

Step 2. Collect Phenotype Data

A protocol must be developed to uniquely identify each dog and to uniformly and accurately measure each trait of interest on all breeding dogs and on all or most of their progeny over successive generations. For behavioral traits, this might be the Behavior CheckList (35), while for a trait like hip dysplasia, the PennHIP (36, 37) or extended view radiograph (OFA, BVA, FCI) scores could be used (38). All data should be stored in a secure, uniformly coded, electronic database like IWDR.

Step 3. Identify Heritable Traits

Using the phenotype data and pedigrees stored in the database, the ***heritability*** of each phenotypic trait measured in step 2 must be calculated. The more heritable a trait is, the bigger the response will be to one generation of selection (39). Traits with a heritability of at least 15% are considered good candidates for genetic selection. With accumulating knowledge derived from genomic information, genetic improvement in traits with even lower heritability may eventually be feasible.

Step 4. Calculate EBVs

For the traits selected in Step 3, EBVs can be calculated using specialized software that combines phenotype data with the pedigree structure (25, 40, 41). Models fitted with this software can accurately account for overlap in the genetic background influencing different traits and for external, non-genetic factors that produce variation in phenotypes, such as the season of year or age of the dog when the phenotype was measured. Access to EBVs calculated using this software is available through IWDR.

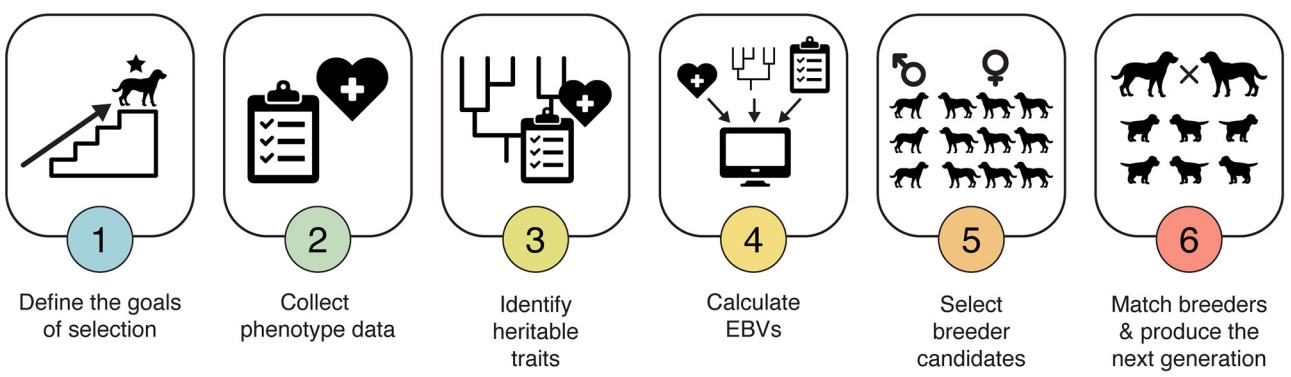

FIGURE 2 | Six-step approach to EBV selection. Implementing an EBV-based selection program can be daunting. By distilling it down to just six steps, each supported by tools and training available through IWDR, this method of making breeding decisions can be made accessible to both working dog breeders and hobby breeders.

Step 5. Select Breeder Candidates

Young dogs with high genetic merit from the EBV analysis in Step 4 should be evaluated in detail to assess their suitability as breeders, with a focus on the whole dog. Metrics considered will typically include suitable conformation, reproductive capacity, health screening typical for the breed and a performance assessment.

Step 6. Match Breeders and Produce the Next Generation

From among the candidate dogs identified in Step 5, mating pairs are chosen, such that weaknesses in one dog are complemented by strengths in the mate. In addition, it is important to choose pairs that maximize the genetic diversity of the breeder pool, minimize inbreeding in litters, and limit the number of progeny any single individual produces in their lifetime (31). A practical guideline is to attempt to limit the average increase in the **coefficient of inbreeding** to no more than 2% per generation.

To achieve this goal, an easily implemented strategy is to limit the number of litters produced by any single parent (42). While inbreeding could be kept to a minimum by allowing each parent to produce only a single litter, this isn't operationally feasible, and thus tradeoffs must be made. One practical solution is to restrict each male to siring no more than 8 litters and each female to producing no more than 3 or 4 litters. In a population producing ∼200 puppies per year, this will limit the rate of inbreeding increase to no more than 2% per generation. We note that, as the rate of inbreeding increase is related to effective population size (39), chapter 4, p. 65], any workable strategy for maximizing the effective population size will limit inbreeding.

IMPLEMENTING AN EBV SELECTION PROGRAM

While the six steps described above provide a high-level perspective on EBV selection, the reality of starting such a program can be daunting. Here, we describe how Guiding Eyes for the Blind (Guiding Eyes, hereafter), implemented their EBV selection program, and highlight some of the challenges they needed to overcome. Guiding Eyes have shared their breeding program data to illustrate this process (43). Their experience illustrates the dynamic nature of any breeding program. The outcome of each of the six steps is not fixed, and often must be revisited and revised based on information acquired as the process evolves over time.

The Guiding Eyes for the Blind breeding colony collectively produces about 520 weaned puppies (about 90% Labrador retrievers and 10% German shepherds) each year. Dogs who do not succeed as guide dogs are either moved to other organizations or adopted out to pet homes, depending on their testing results (44). Currently, Guiding Eyes has 120 active Labrador retriever breeders (82 female and 38 male) and 13 active German shepherd breeders (10 female and 3 male), as well as frozen semen from 20 Labrador retrievers and 13 German shepherds with high selection indexes.

Guiding Eyes started using genetic selection with EBVs in their Labrador retrievers in 2003. Their German shepherd colony is too small to calculate EBVs, but Guiding Eyes is working with IWDR to address this through collaboration and data sharing with other guide dog breeding colonies.

Implementing Step 1. Define the Goal of Selection

Guiding Eyes made the decision to move toward implementing EBV selection in 1995 with the goal of improving health and behavior traits, while preserving genetic diversity. At that early stage, they did not have the data infrastructure needed to identify which traits were most correlated with those outcomes, and thus might be the targets of selection. The collection of phenotype data (Step 2) was critical in making this determination.

Implementing Step 2. Collect Phenotype Data

Guiding Eyes first had to set up a data management system (a relational database) for collecting phenotype, health, and pedigree information, and populate it with information on their dogs. Using this database, Guiding Eyes identified hip quality, elbow quality, soft trachea and allergic/atopic dermatitis as top health reasons for dogs failing out of the program. Although nearly twice as many dogs failed for temperament or behavioral reasons, rather than health reasons, Guiding Eyes did not initially have a useful system for scoring non-health traits. Behavioral trait data was being collected using the Canine Behavioral Assessment and Research Questionnaire (C-BARQ), but the estimates of heritability for C-BARQ measured traits were very low, and insufficient for driving genetic improvement (45).

It took a global collaboration of working dog breeders 10 years to develop a tool for assessing behavioral traits with the standardized terminology, inter-rater reliability, and score resolution needed for genetic selection. The Behavior CheckList, which is the tool recommended by IWDR, is an optimized version of the scoring tool originally used to validate construct validity of the C-BARQ, and incorporates measures known to affect guide dog performance, including noise sensitivity, harness sensitivity, and body sensitivity (**Figure 3A**; **Supplementary Material**) (45). Behavior CheckList scores are assigned by trained personnel with experience in behavioral coding. At Guiding Eyes, behavioral coding has been correlated with behavioral information captured by ECG, accelerometry and gyroscope data on ∼2 month old puppies (46).

The Behavior CheckList was originally designed for assistance and guide dogs, but it may be generalizable to other types of working dogs, such as detection dogs, when augmented with additional job-specific phenotypes (e.g., hunt drive, indication, bite) (47).

Implementing Step 3. Identify Heritable Traits

Traits included in an EBV selection program need to be both relevant to the high-level goals of the program, and sufficiently heritable to respond to selection. For each trait measured in

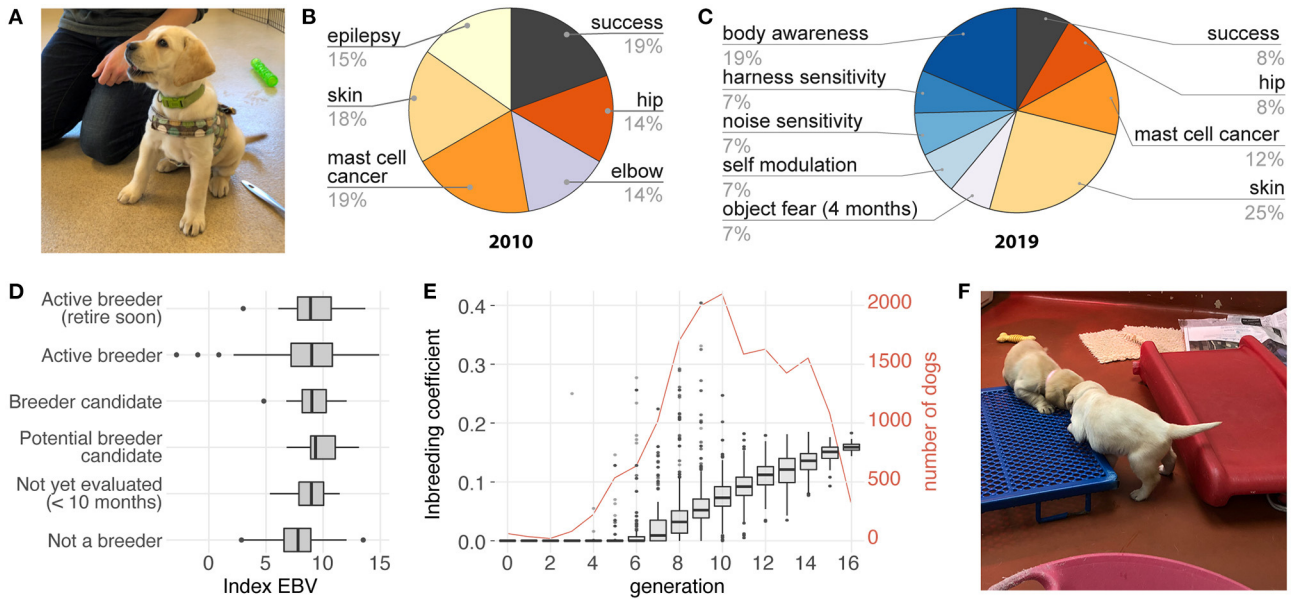

FIGURE 3 | Implementing EBV selection at Guiding Eyes for the Blind. **(A)** The behavioral phenotypes are collected using the Behavior CheckList scored by trained observers during standardized tests and assessments starting at 2 months of age, and continuing through training until about 26 months of age. **(B)** The selection index, which weights each trait based on its importance to the breeding program, has changed over time to include more behavioral phenotypes. **(C)** The current index includes about 50% behavioral and 50% health traits. **(D)** The rate of genetic improvement can be monitored by reviewing the selection index scores for the current population of dogs. Here, dogs not used for breeding have, on average, the lowest scores, while active breeders, including those nearing retirement, have the highest scores, consistent with the increasing genetic improvement expected in a successful breeding program. If genetic improvement plateaus or worsens, the genetic model, data quality, change in testing protocols or criteria, weighting in the index and other influences are reviewed and corrective action taken. **(E)** Inbreeding is minimized by selecting mate pairs that maximize diversity, and by limiting the number of progeny produced by any single individual. Between generation 8 and 16, average inbreeding coefficient increased from 3.4 to 16%, corresponding to an increase of 1.6% per generation. **(F)** To produce high-performing working dogs, environmental factors that influence success must also be addressed. At Guiding Eyes for the Blind, for example, kennels with nursing puppies are enriched with different surface textures, noises, novel objects, and other experiences the puppies will need to be familiar with as working dogs. Image credits **(A,F)**: Elinor K. Karlsson.

the Guiding Eyes population, and collected in the database, the heritability was estimated using statistical models that considered sex, age, weight, and other features when appropriate (**Table 1**).

Implementing Step 4. Calculate EBVs

Guiding Eyes started calculating EBVs in 2003 for two traits: elbow quality and hip quality (**Table 1**). EBVs were estimated using MTDFREML (MTGSAM for binary threshold traits) (48, 49). By 2010, they had collected sufficient data to develop their first overall selection index, combining and weighting EBVs for five health traits, selected because they were most responsible for dogs failing prior to beginning training, and a binary measure of training success (**Figure 3B**). The emphasis (relative weight) placed on each health trait was proportional to the percent of rejections caused by that trait. The standardized weight was calculated by dividing the relative weight by the genetic standard deviation of the trait. To calculate the overall selection index value for each dog, the EBV for each trait was multiplied by the standardized weight for that trait, and the weighted EBVs for all traits then added together.

Selection by EBVs is an inherently dynamic process, because the selection itself changes the frequency of traits in the population, so the selection index is reviewed and revised regularly to focus on traits of highest priority in the current population (**Table 1**). By 2014, Guiding Eyes had sufficient Behavior CheckList data to incorporate EBVs for behavioral phenotypes, starting with thunderstorm phobia and harness sensitivity. Before adding a new behavioral EBVs into the overall index, its utility is assessed by someone knowledgeable about the colony, to confirm that dogs are ranked generally as expected. This less quantitative "sniff test" is important for affirming the real world relevance of the EBV.

Today, behavioral and health traits are equally represented in the Guiding Eyes selection index (**Figure 3C**). Each dog's score on the selection index is the primary tool used to decide which young dogs should be considered as breeders (step 5). EBVs, and the overall selection index score for each dog, are recalculated every 2 weeks to coincide with the selection of new breeder candidates, ensuring that all phenotype data are included in the calculations.

Implementing Step 5. Select Breeder Candidates

Typically, Guiding Eyes replaces about one third of its breeding colony each year. An increase in average genetic merit means that animals in the next generation will have more desirable genetic potential than their parents (**Figure 3D**). While Guiding

TABLE 1 | Heritability and genetic selection at Guiding Eyes.

Trait	Estimate of heritability (%)	No index		Weighting in index				Software used
		2003	2005	2010	2014	2016	2019	
Success	46			20%	23%	35%	8%	R
Health	44			–	–	–	–	R
Health-related measurements								
Elbow quality	63	EBV	EBV	14%	–	–	–	R
Epilepsy	62			15%	12%	8%		R
Soft trachea (STEBV)	61			–	–	–	–	R
Tricuspid valve dysplasia (TVD)	56			–	–	–	–	R
Hip quality	52	EBV	EBV	14%	–	–	8%	R
Skin (Allergic/atopic dermatitis, otitis, etc.)	39		EBV	18%	21%	21%	25%	BLUPF90
Mast cell cancer (age of onset)	28			19%	11%	14%	12%	R
Behavior-related measurements								
Activated by stress (puppy test)	56			–	–	–	–	BLUPF90
Noise sensitivity (puppy test)	54			–	–	–	7%	BLUPF90
Thunderstorm phobia	50			–	15%	–	–	R
Inhibited by stress (puppy test)	48			–	–	–	–	BLUPF90
Harness sensitivity (2-trait with IFT EBV)	47			–	18%	10%	7%	BLUPF90
Body awareness (3-trait with IFT EBV)	36			–	–	12%	19%	BLUPF90
Self-modulation (puppy test)	34			–	–	–	7%	BLUPF90
Object fear (puppy test)	32			–	–	–	7%	BLUPF90

Genetic selection with EBVs will be most effective on traits that have a heritability > ∼15%. Heritability measures are specific to a particular population and a particular environment, requiring them to be estimated for each breeding population. Here, we show heritability estimates for the Guiding Eyes for the Blind Labrador retriever population, which range from a low of 28% (mast cell tumor) to a high of 63% (elbow quality). "Puppy test" indicates testing done at ∼2 months of age, and IFT (In For Training) indicates testing done at ∼16 months of age. We also show how traits were weighted in the overall selection index, and how those weightings change over time. "EBV" indicates traits for which EBVs were calculated prior to the development of the selection index. A dash indicates a trait not included in the selection index.

Eyes prioritizes dogs with a high selection index values as breeder candidates, the decision to keep a dog for breeding is not based on those scores alone. Each month, 9 females and 3 males (usually 15–17 months old) are selected as breeding candidates and undergo additional behavioral, health and reproductive screenings. Dogs may be excluded based on weight, heritable conditions not captured in the selection index, reproductive abnormalities (e.g., cryptorchidism), primary persistent anestrus or abnormal estrus patterns, or undesirable conformation. In addition, they consider the individual dog's longitudinal behavioral scores and behavioral trends in the litter. Finally, they consider how closely related the candidate is to other dogs in the breeding colony, favoring the less related dogs.

Implementing Step 6. Match Breeders and Produce the Next Generation

When Guiding Eyes matches dogs for breeding, it tries to balance weaknesses in one dog with strengths in the mate. It assesses each potential pairing using three primary criteria: (1) the dogs have not been previously bred together; (2) their progeny would have a lower predicted coefficient of inbreeding compared to pairings with other dogs; (3) neither dog is affected by a genetic disease caused by a known mutation, and, at most, only one of the pair is a carrier. In order to avoid popular sire effects, Guiding Eyes tries to use all stud dogs equally.

GENETIC CHANGE DUE TO SELECTION IN THE GUIDING EYES BREEDING PROGRAM

Overall, the breeding program at Guiding Eyes has been very effective, illustrating the power of EBV selection. Most importantly, Guiding Eyes was able to reduce the number of puppies born each year, from 4.8 to 3.6 pups born, for each successful dog (**Figures 4A–C**). Given the enormous resources required to train even a single dog, this achievement has allowed Guiding Eyes' to more efficiently fulfill its mission of providing high-performing dogs to people with vision loss.

Guiding Eyes saw an improvement in the EBVs for every trait included in the selection index (**Figures 4C,F**). Elbow quality, and scores for behavioral traits, including harness and body sensitivity, and noise sensitivity, all improved (**Figures 4D,E**) The incidence of allergic/atopic dermatitis, idiopathic epilepsy and soft trachea all dropped. When using phenotype based selection, the number of dogs diagnosed with allergic/atopic dermatitis, elbow dysplasia, and idiopathic epilepsy had varied widely from year to year, but once EBVs were employed, a consistent genetic improvement was evident. Throughout the breeding program, inbreeding coefficients slowly increased at an average rate of 1.6% per generation (**Figure 3E**).

Several interesting features are evident in the data. First, environment matters (**Figure 3F**). In 2017 there is a sharp rise in dogs exhibiting moderate and severe noise fear (**Figure 4E**). This

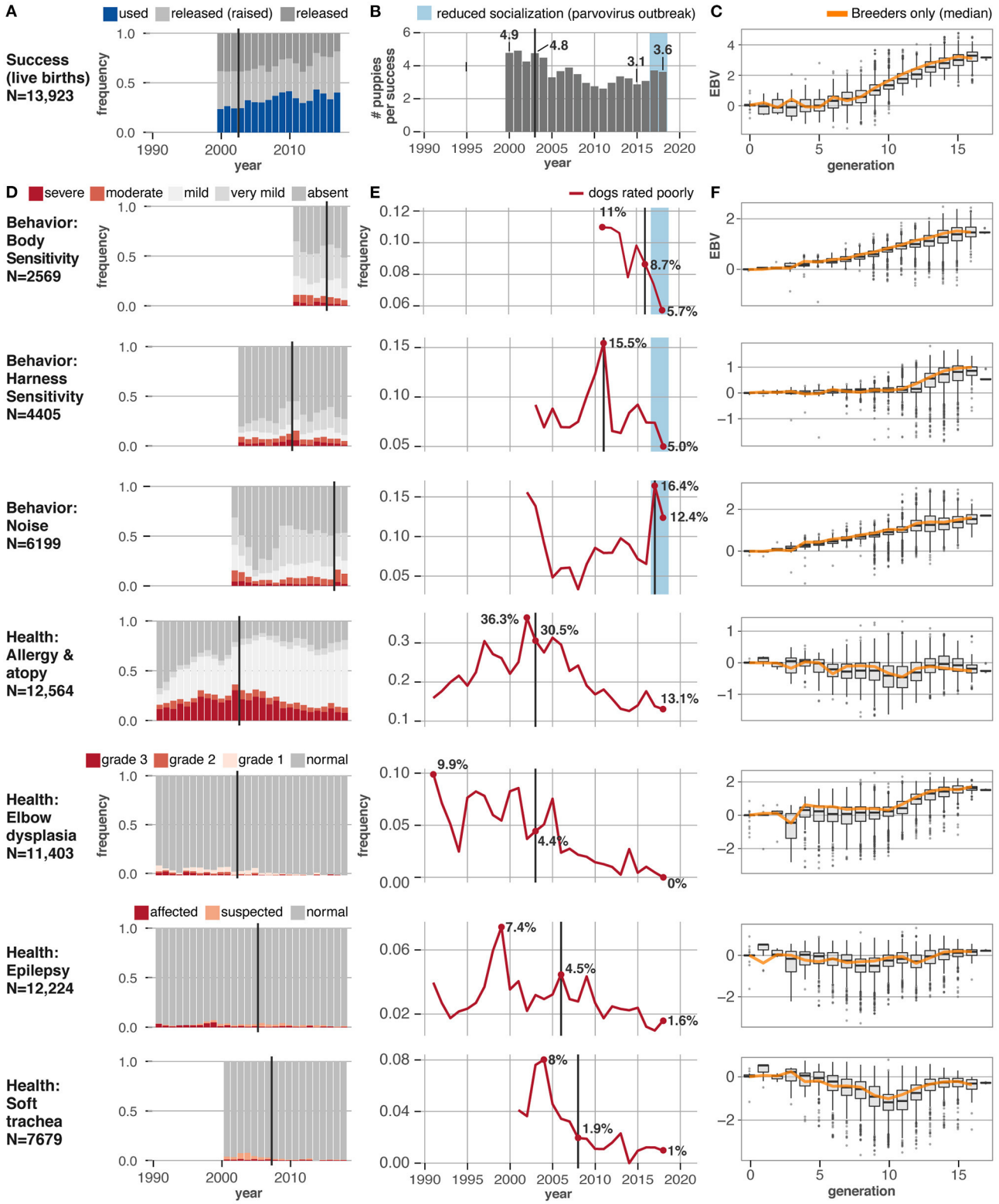

FIGURE 4 | Behavioral and health traits change in response to EBV selection. Eight traits under selection in the Guiding Eyes for the Blind population show varying responses to the onset of selection using EBVs. Vertical black lines show when EBV selection for each trait was started. **(A)** Change in fraction of dogs successfully placed as guide dogs per year, starting in 2000, when the current assessment criteria were implemented. **(B)** With improving success rates, the number of puppies produced by Guiding Eyes for each successful dog has dropped over time. **(C)** The EBV scores for success, as a trait, have increased over the last 17 generations

(Continued)

FIGURE 4 | of selection, indicating an improvement in genetic merit with each successive generation, even if just the animals selected as breeders are considered (orange line). **(D)** Change in relative frequency per year of different phenotypes, starting with the year the phenotype data started being collected. **(E)** Change in the fraction of dogs with a disqualifying phenotype (red lines). **(F)** The EBV scores for each trait over the last 17 generations of selection show increasing EBVs, indicating an improvement in genetic merit with each successive generation. A similar trend in the median EBV scores is seen if just the animals selected as breeders are considered (orange line).

coincides with an outbreak of parvovirus in the breeding facility, which shut down the early socialization program for puppies. This program was designed specifically to expose dogs to a wide range of stimuli, including different noises, during a critical period of development, and its curtailment was detrimental.

Second, how traits are defined for the selection index can lead to unexpected consequences. Between 2010 and 2011, before the Behavior CheckList was in use, the only behavioral metric used in the selection index was a binary trait reflecting whether or not a dog successfully completed the guide dog training program. Selecting for this trait inadvertently increased the incidence of excessive body sensitivity in the population. A closer look revealed that using success as a metric favored dogs who were easy to control, and many of these dogs had heightened body sensitivity. Once the Behavior CheckList measurements of body sensitivity were incorporated into the selection index, the increasing trend in body sensitivity was reversed.

IMPLEMENTING EBV SELECTION WITH IWDR

While the experiences of Guiding Eyes illustrate the potential of EBV selection and how to effectively implement this six-step approach, EBVs have not been widely adopted by working dog breeding organizations because most programs, on their own, have neither the dog population size nor the staff expertise to implement it successfully. To make EBV selection accessible to all working dog breeding programs, regardless of the size of their breeding colony or the expertise of their staff, a different approach is needed. IWDR supports both working dog and hobby breeders of any breed interested in using EBVs to achieve genetic improvement. It offers state-of-the-art tools, expertise, and training that, until now, were accessible to only the largest canine breeding colonies.

Database

For breeding programs, establishing and maintaining a database, and managing data storage, is costly and difficult. IWDR provides a secure, uniformly coded, electronic database accessible through a paid subscription (International working dog registry—dogs serving humanity[1]) from anywhere in the world. IWDR facilitates storing phenotypes, pedigrees, and genetic data.

Phenotyping

Many breeding programs still use non-standardized phenotype scoring approaches that are not ideal for EBV selection. IWDR provides expert training and resources for standardized phenotype scoring, including for behavioral traits via the Behavior CheckList (35).

Tools to Estimate Heritabilities and Calculate EBVs

Breeding programs are often too small to use EBV selection, or lack the required expertise. IWDR stores phenotypes using a standardized codebook, making it possible to pool data from many organizations. Using pooled data, IWDR can estimate heritability and calculate EBVs using all dogs of a specific breed, while keeping the detailed data for each organization secure and private. EBVs calculated by IWDR will be far more accurate than those from a single, small breeding program, because they are based on many more observations, thus enabling all breeding programs, regardless of colony size, to utilize EBVs. With these values, breeding managers can assess which are the genetically most desirable dogs within their colony to keep for breeding, and they can compare their organization's EBVs to the population average, thus quantifying where their dogs rank relative to all dogs of that breed in the database.

To calculate EBVs, IWDR uses the BLUPF90 suite of programs (40, 41). Most health and behavior phenotypes are categorized into five classes, ranging from one (least desirable) to five (most desirable), and are modeled as linear mixed models, with fixed effects included to adjust for the presence of environmental effects known to produce phenotypic variation. IWDR can also calculate EBVs for binary traits by analyzing them as threshold traits using the Gibbs sampling methodology implemented in the BLUPF90 program suite. Once EBVs are calculated and stored into IWDR, they are presented with both an assessment of accuracy and each dog's percentile ranking amongst all dogs from that breed in the database.

Pairing Dogs for Breeding

Selecting dogs for breeding is a complicated task, as EBV scores, predicted inbreeding, and health are all considered. IWDR provides an easy-to-use tool that calculates the predicted inbreeding for a potential litter before the mating is actually done, and summarizes both the phenotype data and the genetic test data available on possible mates. IWDR can also compare EBVs between breeding programs, enabling the exchange of breeding stock with less risk of damaging short term outcomes for dogs. This is critical for balancing selection goals with breeding for improved genetic diversity and population health.

Integrating Genomic Relatedness

Genomic data from either marker genotyping or whole genome sequencing can more precisely define the exact degree of genetic relatedness that exists among pairs of dogs than a pedigree alone (50). IWDR is developing tools that will incorporate the use of

[1] Available online at: http://www.iwdr.org (accessed May 31, 2021).

genomic data into the EBV calculations, thus enabling breeders to work with EBVs estimated with higher accuracy.

BUILDING THE NEXT GENERATION OF GENOMIC TOOLS

Today, it is not possible in dogs to accurately predict health or behavioral traits from genome sequence data alone. For a small number of single-gene diseases, genetic tests are available, allowing carriers of disease risk factors to be identified [although with some important caveats (51)]. Single-gene diseases, however, are just a tiny fraction of heritable diseases, and don't include cancer and other common diseases that are the major causes of death in dogs (52).

The vast majority of diseases, and behavioral traits, are genetically complex, shaped by changes in hundreds, and even thousands of genes, as well as non-heritable environmental factors (53–55). For these traits and diseases, applying selection is difficult without using some aids to improve the accuracy of selection decisions. Active selection of desired genetic variation can lead to unintentional accumulation of deleterious genetic variation due to "hitchhiking" of deleterious alleles physically linked in the genome (56), and unintentional, undesired effects if the genetic variants under selection are pleiotropic, or have effects on multiple traits. Without understanding the genetic basis underlying desired or undesired phenotypes, artificial selection for specific traits in domestic dog breeds can increase deleterious genetic variation (57).

The Working Dog Project and IWDR are working together to build the next generation of genomic tools for dogs, in partnership with dog breeders willing to share de-identified genomic data and phenotypes from their dogs. Genomic technologies have the potential to substantially improve selective breeding in dogs, but it will require extremely large datasets to develop robust, high-quality tools. By working together, and pooling data and expertise, we can develop two new approaches to dog breeding that could dramatically improve the supply of high-quality, healthy working dogs: ***genomically enhanced EBVs (sometimes abbreviated to gEBVs)*** and ***genomic breeding values (genomic EBVs)***.

Genomically Enhanced EBVs

EBVs that incorporate genomic data are known as genomically enhanced EBVs. Compared to traditionally calculated EBVs, genomically enhanced EBVs can increase accuracy of genetic merit predictions by as much as two-fold, because genomic information complements pedigree information (27). In practical terms, this means that the accuracy of well-estimated genomically enhanced EBVs for young dogs can be, in some situations, as accurate as if those dogs had already produced 20 progeny who have already matured to acquire their own phenotypes. Compared to EBV selection, genomically enhanced EBV selection is more effective, especially for traits with low heritability (58, 59).

Using genomically enhanced EBVs can make dog breeding programs more efficient. Generating high accuracy EBVs (>0.80) requires phenotypes for both parents and their progeny, a challenge for late age onset conditions, like cancer and epilepsy. The addition of DNA marker information in the form of genomically enhanced EBVs should increase the accuracy of genetic merit prediction in young puppies, thus enabling more accurate selection decisions to be made before they produce progeny. This reduces the generation interval and costs associated with waiting for animals to mature. In addition, a DNA sample collected from a young puppy could identify, at a very young age, dogs that should not be further developed for a particular line of work, but rather should become beloved pets, avoiding costly care and training.

Genomic Breeding Values

A genomic EBV is a prediction of a dog's relative genetic merit based solely on its genome sequence. No pedigree information is required. With genomic EBVs, a decision could be made to keep a young dog for breeding as soon as a DNA sample can be collected, a method known as ***genomic selection*** (60). Selecting animals based on their genome sequence, rather than waiting to measure phenotypes later in life, can accelerate genetic gain by reducing the generation interval.

While genomic selection offers promise for assessing relative genetic merit among young puppies, literally thousands of whole genome sequenced dogs with their well-measured phenotypes will be needed in one dataset in order to develop the prediction equations (61, 62). Once developed for a particular breed, these prediction equations should enable even the prediction of relative genetic merit of dogs from outside breeding programs or dogs living in shelter populations (63, 64). If sufficiently large datasets of full genome sequences and phenotypes from many breeds can be assembled, prediction equations that work in any dog, regardless of breed, may be feasible (60).

Very Large Sample Sizes Are Essential

The key to developing genomically enhanced EBVs and genomic breeding value technology for working dogs will be assembling very large datasets. Both approaches require studies with tens, or even hundreds, of thousands of dogs, each with phenotype information for traits of interest (60, 65), and coordination between working dog breeders, statistical geneticists, and data scientists. The partnership between IWDR and the Working Dog Project is designed to address this challenge. IWDR is a platform for obtaining both whole genome sequences and uniformly coded phenotypes for tens of thousands of dogs. With consent from the dog breeder, these data, once de-identified, can be shared with scientists with expertise in complex trait mapping and statistical genetics through the Working Dog Project. All data contributed to the Working Dog Project will be part of an open data repository, encouraging even scientists unfamiliar with dog breeding to contribute their skills. No breeding program, on its own, has either enough dogs or the expertise to solve this challenge, but by pooling resources, all working dog breeders can benefit.

CONCLUSION

Large-scale genomic studies, such as those we propose for working dogs, have much broader ramifications outside of improved breeding practices. Genomically enhanced EBVs, for example, can predict which dogs are likely to be high-performing working dogs before the investment of significant resources into their training. With big enough datasets, we'll be able to make these predictions in any dog, including shelter dogs, some of whom might be more suited to a high-energy working dog career than life as a pet—thereby opening up new sources for these high-demand dogs.

Ultra-large-scale dog genomics can also support advances in veterinary medicine. In human medicine, genomically enhanced EBVs are known as polygenic risk scores (23), and are already used to predict risk of heart disease at a young age, when risk reduction through environmental changes is still feasible (66). Similarly, given enough data, we should be able to develop risk scores for complex diseases like cancer and heart disease for veterinary medicine, identifying which dogs should be most carefully monitored, or when interventions should be more aggressive.

Finally, large-scale genomics is the first step in discovering the fundamental genetic basis for health and behavioral traits (67, 68). Aging and disease in dogs show strong similarities to humans, and finding the cellular mechanisms responsible in dogs could provide new clues for treating humans as well (69), ultimately resulting in better diagnostics, therapeutics, and lifestyle interventions for dogs and humans alike.

For complex traits like behavior, which reflect the interaction of genes with the environment, predictions based on genomic data alone will never be perfect. Environment, especially early in life, has a profound effect on the development of the brain. If a mother is not able to perform intrinsic nesting behaviors, or escape from her pups for a while, this stress can lead to aberrant working behaviors in her pups (70). While still in the breeding kennels, working dog puppies develop vision, fear, social behavior, and cognitive abilities, and how these characteristics develop reflects environmental cues. A breeding program that does not provide positive early exposure to a variety of sounds, scents, textures, and visual stimuli will leave their dogs more fearful of the world around them, and less able to perform their job. On the other hand, breeding programs that do provide puppies with a wide range of novel, and positive, experiences in a developmentally appropriate way will maximize the return on an investment in improved breeding practices.

Collaboration and data sharing are essential if we hope to improve the supply of high performing working dogs. Sharing the details, and outcomes, of ongoing breeding programs, including both successes and failures, will help develop better genetic selection techniques for dogs. Furthermore, no single organization can hope to reach the massive sample sizes required to develop the next generation of genomic tools. When searching for the genetic causes of a complex trait, the bigger, the better, and there is no clear upper bound on how many samples are enough (65). By working together, IWDR and the Working Dog Project will promote innovation and collaboration via advanced genomic technologies and open science, and provide the practical tools dog breeders need to implement these advances. This collaborative strategy is the only practical path for realizing the potential of genomics to transform working dog breeding, and to address health challenges in both dogs and humans.

AUTHOR CONTRIBUTIONS

EK, EL, and FLC equally contributed to the formation of the manuscript's conceptual ideas and framework. All authors contributed to writing and editing the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fvets.2021.662429/full#supplementary-material

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GLOSSARY

Coefficient of inbreeding: A measure, ranging between 0 and 100%, of the degree of homozygosity present in the genome of an individual. Animals with low (<10%) or no inbreeding are more genetically diverse than individuals with higher inbreeding coefficients. Animals that are 100% inbred are genetically identical, to the point that tissue like skin grafts transferred from one to another are readily accepted by the body.

Complex trait (or complex disease): Any trait whose inheritance cannot be explained by variation in a single gene. Complex traits (like behavior traits) and diseases (like cancer) are polygenic, shaped by variation in hundreds of genes, and by the environment, and tend to show a continuous range of variation.

Estimated breeding value (EBV): Statistical measure of relative genetic merit of an individual compared to others in the population for a given heritable trait. To obtain an EBV for each member of a breeding population requires collecting pedigrees and an accurately measured trait on at least several hundred or more genetically related animals.

Genetic merit: Animal breeding term describing how an animal ranks relative to other individuals being considered as prospective parents of the next generation of offspring in a selective breeding program.

Genomically enhanced EBV (gEBV): Produced by incorporating genomic (DNA-based) information into the statistical model that generates an EBV; either by improving estimates of relatedness using genomic data and/or by associating genomic data with variations in the desired trait.

Genomic breeding value (genomic EBV): Measure of genetic merit of an individual relative to others in the population using only DNA based information.

Genomic selection: Selection that uses DNA based information; in animal breeding this specifically refers to methods using genomic data (such as SNP markers or whole genome sequencing data) associated with specific trait(s) to directly estimate the genetic merit without first observing the trait in that animal.

Genotype: The genetic complement of an individual inherited from its parents. This term is also used to describe the pair of alleles observed at a single locus in an individual.

Phenotype: The observable characteristics, or traits, of an individual that result from the interaction of genetics with environment. A single phenotype can reflect the influence of many different genes (see complex trait).

Phenotypic selection: Traditional method of selecting which individuals breed based on whether or not they display desired traits.

Polygenic risk scores: a measure of the likelihood that a person's genetic makeup will eventually lead to expression of a particular disease or human health anomaly. Polygenic risk scores are widely used in human medicine and human genetics. The underlying statistical methods for calculating these scores are mathematically equivalent to the methods used for calculating estimated breeding values or genomically enhanced breeding values.

Postzygotic selection: Selection that occurs after fertilization (for example, by providing some adult animals with extra food resources). In contrast, prezygotic selection includes deciding which individuals will mate, and is common in modern dog breeding.

Selection index: Method for determining an individual's overall genetic merit. It is best used for making selection decisions with respect to multiple traits at once by weighting each trait based on its importance to the breeding program.

Heritability: The percent of total variation observed in a trait within a population that is genetically transmitted from parents to their offspring. Heritability can range from 0 to 100%. If a trait is highly heritable, like coat color, it suggests a dog's phenotype is determined largely by genetic factors. Heritability measures are specific to a particular population and a particular environment.

International Working Dog Registry (IWDR): A nonprofit resource consisting of a secure online database storing uniformly coded phenotypic and genotypic information on working dogs. IWDR was formed by experts in the working dog breeding field whose goal is to provide data driven genetic selection tools for dog breeders. Website: www.iwdr.org.

Working Dog Project: Part of the non-profit Darwin's Ark Foundation (DarwinsArk.org), the Working Dog Project promotes ultra-large-scale dog genetic research following an "open-science" model. This approach will advance our understanding of complex behavioral traits and diseases in all dogs, and enable the development of powerful genomic tools for working dog breeders. Website: https://workingdogproject.org/.

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REVIEW
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The Animal Welfare Science of Working Dogs: Current Perspectives on Recent Advances and Future Directions

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Working dogs are prevalent throughout our societies, assisting people in diverse contexts, from explosives detection and livestock herding, to therapy partners. Our scientific exploration and understanding of animal welfare have grown dramatically over the last decade. As community attitudes toward the use of animals continue to change, applying this new knowledge of welfare to improve the everyday lives of working dogs will underpin the sustainability of working with dogs in these roles. The aim of this report was to consider the scientific studies of working dogs from the last decade (2011–2021) in relation to modern ethics, human interaction, and the five domains of animal welfare: nutrition, environment, behavioral interaction, physical health, and mental state. Using this framework, we were able to analyze the concept and contribution of working dog welfare science. Noting some key advances across the full working dog life cycle, we identify future directions and opportunities for interdisciplinary research to optimize dog welfare. Prioritizing animal welfare in research and practice will be critical to assure the ongoing relationship between dogs and people as co-workers.

Keywords: animal welfare, dogs, human-animal interaction, science, sustainability, working dogs

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INTRODUCTION

Confidence in good animal welfare practices has been identified as critical to maintaining public support and the sustainability of industries dependent on animals (1, 2). Working dogs are prevalent around the world and fulfill many roles, adding social, cultural, and economic value to human lifestyles. They are valuable co-workers, providing labor that would be more costly for humans to do (3, 4), or performing specialized tasks that people are unable to accomplish, such as scent detection or as the focus of animal-assisted therapy (5, 6). Despite their value, many working dog providers only graduate around half of the dogs bred or recruited to their programs to operational working service, indicating inherent wastage (7).

Over the last 10 years, there has been growing scientific investment to better understand all aspects of working dog genetics, rearing, training, and functional performance in areas as diverse as scent detection, therapy, mobility, and safety with a view to improving canine performance, welfare, and program efficiencies [(7–11)]. Animal welfare science has also developed in the last decade, with the most recent update to the Five Domains Model adapted

to include human-animal interactions, released in 2020 (12). Understood as *quality of life* or *how the animal is feeling*, animal welfare can be recognized as the lived experience of an animal. An animal's welfare is informed by positive or negative experiences across the domains of nutrition, environment, physical health, behavioral interactions; animal welfare scientists measure indicators of these experiences and the animal's mental state to assess animal welfare [(12–15)].

Hampton et al. (16) suggest that industries with strong scientific investment are more likely to retain community approval for their animal use, also referred to as social license to operate. The role of scientific research to inform modern animal management practices has also been identified as critical to industries reliant on animal use, including working dogs (7). Across private, government, assistance and service, racing, livestock herding and guarding working dog sectors, risk assessment may identify a generalized lack of transparency, stakeholder engagement and sharing of evidence-based best practices or standards to ensure the wellbeing of working dogs at the operational level (7). Where industry practices do not meet community expectations, the social license to operate may be revoked, resulting in industry disruption, or cessation or that type of animal use (16)). Examples from the last decade include interruption to greyhound racing and the phasing out of exotic animal circus performances in many locations globally (17, 18). Animal-reliant sectors that have transparency of animal care and management practices, demonstrate genuine engagement that leads to trust with their stakeholders (including the general public). Sectors which are science-informed appear more resilient to media exposés and loss of social license resulting in industry disruption (16). The ongoing use of working dogs is therefore more likely to be sustainable when operators have a strong record of independent scientific research and consequently function using evidence-based best practices that demonstrate how animal welfare is monitored transparently [(7), Hampton et al. (16)]. In the case of working dogs today, animal welfare largely reflects the interplay between three key components: the individual dogs, human attitudes and behaviors, and the physical environment, including facility management practices.

Recognition that dogs are sentient animals, possessing intrinsic value beyond their consideration as possessions, equipment or working contribution is being reflected in changes to legislation and politics globally (e.g., Australia, European Union, New Zealand, Canada, United States, and United Kingdom) (19–22). This shift is representative of a change in our relationship with these animals and the importance we place on their wellbeing and feelings (23). Although the scientific understanding of sentience and animal welfare science are interlinked concepts, the relative importance of species' characteristics is still being explored. For example, research to better understand cognitive abilities, evolution and selection, biological functioning, affective states, natural living, measurement of experiences, observation of behavior and social relationships, or other elements to reflect the lived experience of animals to inform animal management practices [(23–25)]. Concern has been expressed that animal welfare science has focused on optimizing performance and productivity of animals for the benefit of humans, rather than understanding the lived experience, needs and interests of animals [(26, 27)]. This may reflect the economic motivations tied to the sources of research funding [(27–29)]. For some industries, it could be perceived that scientific input is engaged with an exploitative motivation, rather than protective, with little focus to increase understanding, empathy and compassion toward animals [(25, 27, 30)].

Among the concerns in relation to the welfare of working dogs shared by media in recent years, the issues of animal consent and vulnerability appear to be gaining momentum. These issues have not only been observed in relation to working dogs in the last decade. For example, arguments have been made with regard to chimpanzees as vulnerable subjects in research on the basis of confinement, dependency and communication barriers [e.g., (31)]. This has extended into legal discussions, where animal protection by law has historically existed only to the degree that animal and human interests coincide (32). However, the last decade has given rise to cases where non-human animals have been identified as "sentient and vulnerable beings in need of a legal voice" and attributed rights, challenging law previously considered an anthropocentric institution [e.g., (33, 34)]. These trends across different disciplines reflect the attitude shift of concern for animals present among citizens. Identifying vulnerability leads to moral obligations and duties of justice (35). Industries reliant upon animals, including working dogs, will need to be pro-active and transparent in assuring their animal production and care practices do not disappoint community expectations if they wish to have sustainable participation of animals in these roles (1, 7, 36).

The contributions of research to working dog welfare over the past 10 years can be found in scientific publications across all the domains of animal welfare. Researchers engaged with, or based within working dog providers, are generating scientific evidence across fields as diverse as animal behavior, stress physiology, genetics, and technology to learn more about what working dogs need and want, and to optimize performance in the specialized tasks we require of them. Determining whether an animal use is acceptable is often complex, involving consideration of elements such as sociocultural, economic, environmental, both human and animal health, and other factors (37). Science provides a way to help us understand the mental and physical effects of animal use on the animal, informing practices, legislation and decisions relating to animal lives (15).

The aim of this report was to capture key scientific advances relating to the animal welfare science of working dogs discussed by the authors and colleagues at the Wallis Annenberg PetSpace Leadership Institute workshop in 2020. In this paper, we have identified and reviewed these scientific studies of working dogs from last decade (2011–2021), with a particular focus on their relation to modern ethics, human interaction and the five domains of animal welfare. Using this framework, we were able to consider the recent advances in understanding across the full working dog life cycle. This analysis has identified future directions and opportunities for interdisciplinary research to optimize the welfare and

assure a sustainable co-worker relationship for people and working dogs.

A FRAMEWORK TO INVESTIGATE RECENT WORKING DOG WELFARE ADVANCES: AREAS OF FOCUS

Modern Ethics

For decades, the major impetus in investigating and evaluating the roles of animals working with people has focused on the human portion of the equation. Although the past couple of decades have seen great progress in assessing the welfare of working dogs (7, 12), there continues to be a disparity in how these services are valued and evaluated from both the human and animal perspectives. It is evident that in the early years, even with good intentions, most of our expectations emphasized the value of these services for humans, overshadowing the impact of the work on the animals themselves (29). Today, we are seeing a stronger trend to assure reciprocal assessments on both sides of the service partnership. Animals that work with people should have the ability to form meaningful relationships in their lives and an ability to live their lives fully, irrespective of their work activities. In an optimal scenario, the animals' work activities should be enhancing their quality-of-life experiences.

It behooves those involved in training and providing services alongside working dogs to prioritize both ends of the leash to ensure welfare and the value of the experience is more reciprocal. Although some assume that working dogs enjoy their work, the animals are typically not asked if they want to participate in the work that they do. They are just engaged, with consent assumed. Although, it seems today that more attention is given to ascertain if the animal seems comfortable in their position, there continues to be a lag in objectively assessing the welfare of working dogs (29).

Numerous researchers and scholars of ethics and animal welfare have stressed many ethical concerns that professionals need to consider in working with service/assisted therapy animals [(38–43)]. It is important to appreciate that if these working experiences cause an animal to have little control over their daily life and bring discomfort, this can induce unhealthy stress. For example, Burrows (44) reports that, early on, some dogs that were used as service dogs for persons with autism were tethered next to the child for an unrealistic amount of time. Due to the lack of awareness by some of the families, Burrows (44) reported that the dogs within this study experienced undue stress from their interactions.

When addressing the welfare of working dogs, we must consider the ethical parameters of how to judge the process to make ethical decisions that are in the best interest of all those involved. A starting place is integration of a plan into the decision-making process so that we will act with a sense of integrity (45). Making appropriate decisions that consider the multi-dimensional aspects of these interactions for both humans and animals should be the cornerstone of initiating and guiding the process. Within the literature there are numerous ethical models that could be applied to one's decision making to effectively reflect on the work of service or therapy animals. Each of the models considers dilemmas from a distinct prism. The "ethics of care" approach strives to respect all parties involved by placing emphasis on sustaining relationships and the bond that is established (46). The primary focus of this model highlights the working relationship and the trust that is forged between the animal and all parties, as well as the animal's vulnerability. Within this model, whether the animal is provided with enriching quality of life experiences should be considered.

The "rights approach" primarily focuses on protecting and respecting the rights of all parties involved. This ethical approach assesses not only the human benefits derived from the relationship but also the pros and cons from the animal's perspective (47). Finally, the "utilitarian approach" uses a cost-benefit analysis that determines what we should act upon next, based on all the morally relevant consequences (usually harms and benefits for sentient individuals) of the actions available to us (48, 49). Within this model, it is simple to begin to address what are the costs that the animals might experience due to their work and daily experiences. The utilitarian approach does encourage evaluating the benefits that could also occur as a result of the actions. In following this approach, we must ensure that the costs and benefits are assessed objectively, for both the humans and working dogs alike. Such assessment should be robust, using multiple validated measures (physical, behavioral, and physiological) to ensure objective assessment of animal welfare (50).

The five domains (nutrition, environment, physical health, behavioral interactions, and their impact on the animal's mental state) of animal welfare (12) can provide a useful template to determine how the interactions and the working experience impact overall well-being. While not an ethical model, the "Five Domains Model" for animal welfare (12) offers an excellent perspective to assess the well-being of an animal by evaluating how the animal's physical and functional experiences impacts their emotional state. According to Peralta and Fine (46) the Five Domains model can be particularly useful in assessing the possible negative and the positive effects that the working relationship has on an animal's well-being (51). The model promotes the need to emphasize opportunities within each domain that lead to positive affective states (12). One needs to assess each of the domains to ascertain if any of the environmental, social, and physical interactions of working impact specific domains and directly or indirectly affect the animal's mental state.

These ethical decision-making frameworks can be applied to assess what should be considered to ensure that all parties' well-being is taken into consideration. As noted earlier, animals truly do not have a voice regarding their engagement. However, we believe that priority attention must be given to their welfare to assure quality of life. It is incumbent upon all practitioners who work with dogs, as well as researchers, to constantly ask questions about the human-animal relationships (established or being established) to ensure that the engagement is not one-sided, and that everyone's well-being is taken into consideration. This paradigm shift to recognize dogs as our co-workers and the application of ethical principles from human workplace

settings (e.g., healthcare) to offer greater protection to working animals, reflects a change in moral understanding that has ethical implications for working with animals (52).

Human Interaction

Attachment

While links between human attitudes, their relationship to behavior toward animals and the impact of human behavior on animal welfare has been studied in other animal-use contexts, such as farmed livestock (53, 54), there has been less focus on these relationships in relation to working dog and handler teams. However, beliefs and perception of people working alongside working dogs have been shown to be valuable in identifying animal welfare issues (55) and can be critical in shaping the success of some working dog partnerships, such as those between guide dogs and people who are blind or vision impaired (56).

Working dogs have been shown to perform differently for various handlers (57, 58), with implications for operational decision-making, such as working dogs having one or multiple handlers. This performance difference is likely underpinned by the interplay of canine and human personalities, as well as strength and style of attachment between the dog and handler (59, 60). Handler beliefs can impact canine work performance, as demonstrated by Lit et al. (61); when handler expectations were manipulated in an applied environment, alerts by scent detection dogs were impacted. Interestingly, another scent detection study that manipulated handler stress levels showed that working dogs showed improved performance when their handlers' anxiety levels were elevated (62). Such dog-human dyad studies often lack generalizability due to small sample sizes and are regularly taken from one workplace or population of dogs. An opportunity for future collaboration between multiple working dog providers, following the collaborative replication model established by programs such as Many Babies, Many Primates and newly established, Many Dogs (63, 64)), would allow for more robust testing of importance phenomena relating to the human-dog working team's performance and its relation to working dog welfare.

Training Methods and Equipment

Using only reward-based (positive reinforcement) training methods has been found to be more effective than use of aversive, compulsive, punishment-based (e.g., shock collars) or mixed methods. The use of only positive reinforcement results in more optimistic dogs with faster learning and more consistent behavioral responses who experience less pain and suffering, as well as reported lower incidence of aggression, problematic behaviors (e.g., unwanted barking), and symptoms of negative affect (65–69). Many people persist in using aversive methods when training their dogs, despite the known risks to canine welfare (66). A comprehensive review of modern working dog training has been provided by Hall et al. (70) within this special issue.

In many instances, the equipment used while working with dogs, such as collars, leads and harnesses, have not undergone much change in the past decade. The increasing use of pressure sensors, accelerometers and kinematics can offer new insights into how existing equipment impacts dogs when interacting with people [e.g., (71, 72)]. Given the emergence of new textiles and materials that may be stronger and lighter than traditional equipment, as well as nanotechnology, and smart textiles incorporating wearable electronics (73), we identify this as a future area for review and development.

Human Expertise

Humans are often flawed in accurately assessing our own skills and abilities. For example, the better-than-average-effect is a form of illusory bias exhibited across a wide range of competencies, such as driving, environmentalism, and even parenting (74). The effect is seen when people self-assess their capabilities upward, rating themselves better than reality and how others would rate them. Emerging evidence suggests a similar effect may be present in relation to how we perceive ourselves as providers of canine welfare (75). This highlights the importance for evidence-based education programs for all people involved with working dogs and role that external auditing should perform in quality control.

The Dunning–Kruger effect (76) is described in social psychology as the ignorance of ignorance. That is, people lack the knowledge and awareness to recognize what they don't know about a topic. The effect means that those with very little knowledge about something will often believe themselves to have high expertise in that area, preventing them from recognizing mistakes. Understanding how these aspects of social psychology relate to attitudes and behaviors toward dogs, as well-developing best practice, evidence-based professional knowledge transfer for people involved with working dogs is identified as an opportunity for future research.

Nutrition

Provision of Food and Hydration

One of the basic tenets of animal welfare is the freedom from hunger and thirst (51, 77). The provision of adequate food and water is necessary for sustenance, but when considering the welfare of working dogs, this requirement must be viewed through a different lens. Rather than avoiding the negative welfare effects of inadequate nutrition, or settling for merely adequate nutrition (51), the focus should be on enhancing the positive impact of optimal nutrition. In addition, the knowledge base continues to expand and new information to support the working dog must be considered. Working dogs have increased nutritional demands due to the nature of their work. Detection and protection dogs often work in adverse environments and are engaged in physical activity that can lead to dehydration (78–80). Even 15 min of retrieving a ball can lead to fluid loss and detectable dehydration (81). The research over the last decade has particularly contributed to improving our understanding of optimizing hydration in working dogs.

Working dogs are selected for high motivation to engage in their trained task (e.g., searching for a trained odor or apprehending a fleeing suspect). When engaged in tasks that are rewarding or stimulating, these dogs will override the physiologic signals that drive thirst and are critical in preventing dehydration. Even mild to moderate dehydration impairs cognition, decreases alertness, and increases fatigue in humans (82). The effects of

dehydration on cognition and fatigue have not been studied in the dog. Adequate hydration is also essential for control of body temperature. Unlike humans and horses, dogs do not regulate body temperature through sweating. Dogs rely on panting for heat exchange (83) and therefore can be at increased risk of heat-related injury when dehydrated (84). In working dogs, heat injury is recognized as a major and preventable cause of morbidity and mortality (85, 86). Hydration research represents an area of focus, due to the impact of inadequate hydration on performance and welfare and the ability to positively impact hydration in active working dogs.

The human partner of the working dog must be the advocate for the welfare of the dog, which translates to developing strategies to maintain and enhance hydration. One of the simplest approaches is to interrupt the dog during work to provide a hydration break. The dog may still be more focused on work than its physiology, therefore strategies to encourage drinking may be necessary. Although traditionally electrolyte replacement solutions were not recommended for dogs since they do not lose electrolytes through sweat (87), recent studies have suggested that electrolyte replacement solutions can be safe, palatable and may enhance heat tolerance in working dogs (79, 80). The benefit of electrolyte solutions does not appear to be a result of increased palatability and fluid consumption, because flavored water did not show the benefit and may lead to adverse effects (i.e., increased muscle damage) (80). The benefits of electrolyte solutions may be replacement of electrolytes lost in saliva during panting and in urine during exercise (79, 80, 88). On the other end of the scale, excessive water consumption can result in "water intoxication" and the associated dangerously low blood sodium and even death (89). Typically, physiological responses prevent continued water intake, but highly motivated dogs may override the signals, or may consume excessive water during swimming or playing with water (e.g., chasing a hose). This is another setting in which the welfare of the working dog will be directly impacted by the handler's awareness.

Like the requirement for hydration at a level commensurate with the work expected of a working dog, nutrition for optimal welfare extends beyond providing calories. In its simplest form nutrition should be a balance of protein, fat, carbohydrate, fiber, and essential vitamins and minerals to sustain life. For an active working dog, the physical demands alter the nutritional requirements (87). Protein requirements are increased to help build and support muscle that is being used in the work tasks (87, 90). For dogs that require endurance activities, higher fat content in the diet is required (87, 90). In addition to the type of food provided, the recommended frequency of feeding is based on the type of work. Dogs that compete in sprinting or intermediate distance activities may benefit from a 20 to 30% reduction in calories 24 h prior to activity. It is recommended that dogs undergoing vigorous activity are not fed in the 8 h prior to or immediately following the activity. Endurance athletes may require twice daily feeding (87). The understanding of working dog nutrition is a continually evolving field, and a comprehensive review is beyond the scope of this paper; for a recent review of working dog nutrition, see Zoran (90).

Quality of Food

Animal nutrition is a field prone to the application of current human dietary trends to animals. The motivation behind these feeding practices may be to appeal to human purchasers, but can also lie in an attempt to increase the nutritional benefits to the dog (91), conversely, the use of non-traditional diets may put both humans and animals at risk of disease. Two common feeding practices that have been associated with adverse health effects are the use of grain-free diets and raw meat diets. Although still controversial (92), studies suggest that some dogs fed a non-traditional diet (grain-free with non-traditional legume-based protein sources) have an increased risk of dilated cardiomyopathy (93, 94). Diets based on raw meat are popular among animal companion owners (91), however, the Center for Disease Control and Prevention (https://www.cdc.gov/healthypets/publications/pet-food-safety.html), the United States Food and Drug Administration (https://www.fda.gov/animal-veterinary/animal-health-literacy/get-facts-raw-pet-food-diets-can-be-dangerous-you-and-your-pet) and veterinary organizations (such as the American Animal Hospital Association [AAHA] https://www.aaha.org/about-aaha/aaha-position-statements/raw-protein-diet/ and the American Veterinary Medical Association [AVMA] https://www.avma.org/resources-tools/avma-policies/raw-or-undercooked-animal-source-protein-cat-and-dog-diets) have all issued statements warning against the use of raw pet foods due to the hazards of microbial contamination as well as challenges with creating an appropriately balanced diet. Diets for working dogs should be based on nutritionally sound formulations that are demonstrated to be safe for the dog and the canine handler/owner. One strategy to avoid unrecognized nutritional deficiencies and address the welfare benefit of providing a varied diet (12) may be to rotate diet formulations.

In addition to the basic nutrients, functional foods (those that provide benefits beyond nutritional value) and dietary supplements may have a role in supporting health and wellbeing of the working dog. Dietary supplements represent a rapidly growing industry and topic of great interest, with limited clinical trials. Most supplements are designed to reduce inflammation and improve joint health, a relevant impact for working dogs where osteoarthritis is a common occurrence (95). Currently, the supplements with the most scientific evidence of efficacy are the omega-3 fatty acids (96). The balance of omega-3 fatty acids is important for cognition and as an anti-inflammatory, particularly for management of osteoarthritis. Other functional foods may also have a role in supporting the wellbeing of working dogs (97) but more research is necessary. Beyond foods and dietary supplements, one of the most efficacious approaches to minimize inflammation and pain associated with osteoarthritis is weight control.

A greater problem in modern working dogs is not inadequate calories, rather, an excess of calories. Obesity is a frequent problem in pet dogs (98, 99) and is surprisingly common in working dogs. The optimal body condition score of pet dogs is between a 4 and 5 out of 9 (100). Working dogs' body condition score should be between a 3.5 and 4.5 out of 9. The impact of carrying excess weight is multi-fold. The added mass

increases the effort and energy required for activity. Fat is an insulator that can reduce surface heat loss and increase the risk of heat injury. Additionally, adipose tissue is metabolically active and is responsible for the release of inflammatory cytokines that contribute to the progression of osteoarthritis and other inflammatory conditions. In a longitudinal study of Labrador retrievers, a difference in a body condition score of 5 out of 9 vs. 7 out of 9 translated to a lifespan of almost 2 years longer (101).

Physical Health

The physical health of a working dog must be considered from the time of birth or recruitment, throughout the dog's working life and into retirement. Some breeds of dogs as well as individual dogs do not have the physical structure to safely participate in the required tasks of some working roles. For example, a brachycephalic dog that is unable to effectively pant will be at high risk for heat injury during exercise (102). Likewise, a dog with hip dysplasia will not have the structural stability to serve pain-free as a guide, mobility assistance, police, or search dog (103).

Preventive care is critical to maintain working dog health and an example of minimum requirements are described in the AAHA recommendations (104). The environment in which the dog works will dictate the specifics of care; however, all working dogs should have veterinary examinations at least annually. Disease prevention includes vaccination with the core vaccines as recommended by AAHA (105) and inclusion of vaccines for infectious diseases like leptospirosis, canine kennel cough complex and canine influenza based on individual, geographic and environmental risk factors (106). All working dogs should have a comprehensive parasite control program to address both internal and external parasites. Based on the mortality associated with gastric dilatation and volvulus documented in the US military working dog program (85), prophylactic gastropexy should be considered in large breed, deep chested working dogs. Current minimally invasive techniques (107), and limited complications (108) support the welfare recommendation to perform this elective procedure in dogs at risk. Other management decisions, such as spay or neutering working dogs, may also be associated with impacts to health and longevity in breeds such as Labrador and Golden Retrievers [e.g., (109–111)]. The role of the veterinarian in maintaining a low-stress environment during delivery of preventive care cannot be over emphasized. Despite the benefits of the medical care, aversive experiences associated with veterinary visits can negatively impact the welfare and subsequent performance of the working dog. Many of these dogs are highly arousable and minimal physical restraint or early implementation of chemical restraint or anxiolytics is now recognized as standard of care (112).

Physical fitness is an important welfare consideration (12). The implementation of a fitness program requires that the dog is physically capable of the exercises, the environment is safe for performance of the exercises and the training protocol creates a positive experience for the dog. A foundational fitness program has been described for working dogs (10). Any canine fitness program should include flexibility, body awareness, endurance (both cardiovascular and muscular), strength, and mobility. The intensity of the program should be gradually increased in response to objective assessments of the dog's performance, with safety for the dog and the handler paramount. A balanced fitness program will also include mental fitness as the dog learns new behaviors, develops resilience to environmental distractions and increases focus during the exercises (113). The benefits of fitness extend beyond the mental and physical stimulation associated with the training; a fitness program can aid in injury prevention, speed recovery from injury/illness and provide an opportunity for positive human-dog interactions.

Environment

Working dogs can be deployed across a wide range of different environments, from therapy room, to snowy forest or hot desert. The welfare of the dog is dependent on the human partner, which translates to providing a safe location when not working (i.e., in a home environment, during transportation or kennel facility), recognizing early signs of overexertion, disease, dehydration and thermal stress. In the US, kennel facilities, whether in a home or in agency housing are required to meet accepted current USDA Animal Welfare Act guidelines. See Animal Code of Federal Regulations: Title 9, Volume 1 January 1, 2016 (https://ecfr.io/Title-9). Additional kenneling and care standards are under development (https://www.nist.gov/osac/dogs-sensors-subcommittee; http://www.asbstandardsboard.org/published-documents/dogs-and-sensors-published-documents/). In addition, environmental enrichment, access to exercise and play (with people and with other dogs) all enhance the welfare of the working dog (114).

Thermoregulation and Heat Injury

Heat injury can be localized, for example blistered paw pads from hot surfaces, or systemic hyperthermia from exertion, hot environments, or inability to effectively cool. Systemic hyperthermia can lead to various degrees of systemic insult from heat stress (discomfort and physiologic response) to heat exhaustion (mild to moderate dysfunction with dehydration and decreased cardiac output) to heat injury (elevated body temperature with organ injury) to heat stroke (115, 116). Traditionally, heat stroke is defined as an elevated body temperature (>40.6°C; 105°F) accompanied with signs of neurologic dysfunction and the risk of multiple organ dysfunction (115). During activity, working dogs have been reported to maintain and recover from body temperatures above 41.1°C (106°F) without evidence of heat injury (80, 117). Prevention of heat injury needs to focus on a safe temperature-controlled environment for the dog, control of heat generating activity, and effective heat exchange. A common breach in welfare occurs when a dog is left in a closed vehicle in a hot environment, whether inadvertently or through a failure of cooling systems (118). Some dogs are highly motivated by the mental stimulation of their work and this may override normal physiologic triggers that drive thirst (80) resulting in exertional heat stroke. The environmental temperature and humidity should be considered when planning dog training sessions or determining work cycles to decrease the risk of heat injury (119). Finally, diseases or

dog training equipment that obstruct the flow of breath (e.g., laryngeal paralysis, tight muzzles), inadequate hydration and lack of physical conditioning will all predispose dogs to heat injury (117).

Transportation

Transportation is a common occurrence for many working dogs and has been shown to be stressful and resistant to habituation if familiarization does not occur *via* positive early exposure in life (120). Of particular importance to note is the regular occurrence of working dogs being forgotten and left in unattended vehicles for extended periods, leading to their death when heat and dehydration impact without sufficient ventilation, hydration or cooling in place. In response to the climate crises and global warming, vehicle transportation has been identified as a risk for dogs, even in areas not traditionally considered hot, such as the United Kingdom (121).

Behavior

Behavioral issues are a major contributing factor to the high failure rates in working dog programs (8). Reducing behavioral wastage (the proportion of dogs bred or recruited to train that do not reach operational status due to their behavior) by improved assessment and tailored support for dogs will bring welfare benefits (122). Research considering the behavior of working dogs over the past decade has largely focused on tests to improve the selection and performance of working dogs, with the aim of increasing program success rates, currently reported to be ∼50% across different working dog sectors (3, 7). This focus on behavior has included assessment of behavioral characteristics considered predictive of suitability to work (122, 123); the genetics of working dog behavior (124); maternal care in working dog breeding programs (125); and development and testing of cognitive skills [(126, 127)]. The use of technologies to capture and support behavioral observations such as activity monitoring and bio-metric sensors, in conjunction with algorithms (e.g., machine learning) to process large data sets are also being deployed with the goal of enhanced screening of working dogs (128).

Although some behavioral assessments report good predictive validity (42), aspects of research-driven behavioral assessment that may obfuscate their translation to industry practice include inter-rater reliability, and the reliability and construct validity of behavioral measures (129). Terminology used to describe behavior can also vary widely between and across industry sectors, potentially creating confusion for researchers, working dog trainers and handlers alike (7, 130). Some dogs that fail out of one program may be suitable for other careers, prompting programs to consider developing a co-operative approach (8). Not all dogs that fail to reach operational status are considered to exhibit behavior suitable for rehoming to non-working placements. Community attitudes and media attention have prompted changes in some sectors that historically euthanized or abandoned working dogs as an end point to their training or working life [e.g., Royal Australian Air Force Wilson: (131); US Military: Alger and Alger (132, 133)]. This indicates the influence of community attitudes and the media in driving industry change to retain social license to operate. However, without research reporting on the behavior and welfare of working dogs that have career-transitioned, it is unclear how well they adjust to rehoming away from training or work. This is an important future direction for investigation to extend our understanding of dogs bred or recruited to work to full-life cycle consideration.

Further work to identify and understand behavioral indicators of working dog welfare is needed. While many studies have sought to advance the "production of better dogs" (127), it is time to focus on extending our identification of behavioral indicators of affective state and welfare specific to working dog operational environments, kennel facility and home settings (134). The importance of drastic social and physical environment change inherent in many working dog programs has been identified as a welfare concern [e.g., (135)]. New findings in this area, particularly with consideration for the influence of dog personality and coping styles, would be useful to practitioners and regulators in guiding the development and implementation of best practice and standards. For example, identification of the behavioral cues of detection dogs that require rest breaks in airports or understanding how best to transition a young dog from puppy raising home to training kennel, would help guide regulations for optimal welfare during work. The roles of early socialization, provision of agency, and lifetime opportunities to play (with dogs and people) for the wellbeing of working dogs are also important area to investigate that are currently unexplored. Emerging technologies, such as those utilized in bioacoustics and precision livestock farming, may be useful tools in the remote monitoring of behavior and welfare in settings such as kennel facilities and private home environments [(136–138)].

Mental State

Optimal rest and sleep are critical for working dogs. Sleep is associated with emotional state in sentient animals and is necessary for consolidation of learning, immune function, optimal performance and recovery to ensure longevity in working dog roles (139–142). Remote monitoring of canine sleep can be used to alert staff to disruption or change from normal sleep patterns that might impact animal welfare (143). For example, sleep deprivation has been shown to be detrimental to learning, decision making, and promoting negative affective states in rats and humans (144) and can also interfere with canine physiological stress responses such as cortisol (145). In addition to getting enough good quality sleep, it is critical for working dogs' social and mental needs to be met (51, 146).

The term *enrichment* has been widely used to describe animal care or management practices that help overcome deficits inherent in an animal's environment or social life. For example, Gfrerer et al. (147) report on the benefits of conspecific interaction for Swiss adult military dogs usually housed in isolation. Rather than interpreting this activity from the human perspective as a training or enrichment exercise, this compensatory social exposure might be reframed to reflect that its function is enabling the dogs to meet their psycho-physiological and behavioral needs for interaction with other dogs for mental wellbeing. It may be useful to reframe our thinking of social, environmental and mental enrichment as

"meeting critical needs," rather than perceiving such programs as non-essential extra, if resources allow.

The capacity for animals to engage freely with their environment under their own motivation is referred to as *agency* (148). Promoting agency in animals can improve behavioral diversity and have a positive effect on their welfare (149), but can prove challenging in some working dog settings. For example, it may not be appropriate for a working seeing-eye dog to explore dropped food or approach another dog to play. Nonetheless, identifying and supporting regular opportunities for working dogs to exercise agency and increase behavioral diversity in both environmental and social contexts is an opportunity for future studies. One activity that has been shown to induce positive judgement bias in dogs, is nosework (150). Letting dogs engage in olfactory-based sniffing activities resulted in them exercising autonomy and agency, resulting in increased optimism (150).

Working dogs have demonstrated long-term behavioral resilience after deployment in acutely stressful situations, such as the search and rescue dogs deployed at the site of the September 11, 2001 terrorist attacks (151). Other studies, such as that by Wojtaś et al. (152), suggest that rescue searches are stressful events to working dogs, demonstrated by elevation in salivary cortisol. The use of salivary cortisol in canine studies is widespread, yet it is a measure that can be influenced by a wide range of factors, making direct comparison between individual dogs and studies very hard (145). Our ability to differentiate dogs' acute and chronic cortisol responses as excitement or distress relies on interpretation offered by additional measures including behavioral observations and additional physiological indicators such as heart rate variability and immune function (135). This highlights the need for further investigation and assessment toward routine inclusion of multiple reliable and robust measures when assessing the welfare of working dogs.

DISCUSSION

Full Life Cycle Consideration

Assessment of working dog welfare should occur routinely throughout working life (153–155), with regular reviews of exit data (when dogs are discontinued from training or retired from work) to look for patterns across time to identify other animal welfare concerns, relating to both physical and mental states [(156–158)]. These initiatives should include consideration for all environments and activities, including those outside of operational working sessions and with transparent surveillance and reporting across the full life cycle. This continuous improvement ethos should include adequate resourcing to be inclusive of breeding, rearing and/or recruitment; housing, transportation and husbandry practices; training techniques and dog training equipment; trainer and handler education; career change and retirement of working dogs.

Scientific Research and Sustainability

Scientific information needs to be readily accessible to compete with other information reaching working dog industry stakeholders (29). Meaningful engagement and improved community outreach by researchers are needed to improve the uptake of research findings into evidence-based best practice. The knowledge deficit model of science communication traditionally used by scientists, centers on the assumption that ignorance is the basis for non-scientists in the community not adopting evidence-based best practice (159). Scientists following this model of science communication believe that one-way dissemination of their scientific knowledge to individuals and groups should be sufficient to prompt changes in their attitudes and behavior (160). The deficit model has been shown to be less effective than alternative bi-directional communication approaches that draw on the social sciences, such as participatory and community-based dialogue approaches (159, 161). This is particularly true in morally contentious areas such as the care and welfare of working dogs (29). When consulted, working dog industry workers have told the authors that scientists were not asking the questions they believed to be most important to industry (135). This is critical as research can be impacted by restricted access to working dog populations, and failure to win the trust of the industry through the way we communicate about our science may compound this.

Researcher access to working dog populations is limited and study cohorts are often statistically small (6). Analyses often draw on group averages, rather than group-based trajectory or latent class analyses widely used in human health research (e.g., Nagin et al. (162)). These techniques allow analysis of subgroups following similar response trajectories within a larger population, which might offer a more meaningful indication of individual preferences, responses and welfare [e.g., (163)]. There are limited opportunities for experimental manipulation with working dogs: kennel and animal management practices and training programs are generally well-established and successful dogs are required to meet operational and business requirements. This reluctance to change practices or participate in research, is seen in other areas where investment takes place over an extended time and the end product has high value (164, 165). Langston (164) notes that "*the role of industries in generating, shaping, and reinforcing norms, in addition to producing products, is often overlooked.*" In the non-profit sector particularly, where resources are limited, this results in experimental change being viewed as a risk to the success of the program.

The tendency for risk-averse industry groups to favor inaction highlights the need for more effective communication strategies between all working dog industry stakeholders if a sustainable outcome is to be achieved. A participatory, community-based research approach where industry representatives and researchers come together to formulate and answer questions of mutual interest is most likely to result in collaboration that fosters a shared purpose, improving uptake of research findings into evidence-based best practice (165, 166). Similar strategies in agricultural contexts found the participatory process gave farmers the analytical tools they needed to think critically and make informed decisions, improving their confidence when explaining the function of innovations to others and the desire to engage in sustainable change (165). This could be achieved by means of workshops to develop a schedule of research initiatives that are publicly, or government funded to better engage scientific researchers with the working dog industry to demonstrate the mutual benefits of collaboration.

Actively contributing to the development of this evidence base is possible by organizations and practitioners collaborating with scientific researchers. When this occurs, funders and researchers should insist that the animal experience is robustly assessed by multiple behavioral and validated physiological measures (29). This change would serve to help balance our understanding of the animal experience in working settings, where historically we have emphasized the human outcomes. Greater interdisciplinary collaboration between researchers (i.e., including animal welfare scientists in working dog research design and teams) will enable this, and result in greater uptake of research findings into practice. Ideally, all granting bodies who fund exploration of the possible benefits to people from working dogs should also fund and require that the working dogs' physical and mental experiences be reliably and robustly monitored and reported.

CONCLUSION

Assuring all stakeholders, including the general community, that the welfare of working dogs is positive will be fundamental to retaining social license to operate across the varied working dog sectors. Good, transparent animal management practices informed by independent science to assure positive animal wellbeing will be needed to underpin a sustainable partnership working with animals in this way. Our understanding of animal welfare science and working dog performance have grown rapidly in the last decade. However, many aspects of working dog welfare have not been studied robustly and are ripe for research, innovation, and improvement.

Opportunities to make valuable contributions to improving the welfare of working dogs through further research have been identified across five domains of animal welfare in this analysis. Scientists working in this field can collaborate, within and between disciplines, to improve the validity of their work by studying composite dog populations and exchanging experiences between working dog sectors. In addition, researchers who to familiarize themselves with updated science communication strategies will have greater success in seeing their work translate to improved industry practices. Psychological studies show us that people tend to assume we are better at things than we actually are. Knowing this, there exists a responsibility to assure the positive welfare of working dogs. This can be achieved by committing resources to study the welfare of working dogs, the use of external auditing, and good science communication that enables practitioners to help shape and stay up to date with new working dog welfare science research.

Regular evaluation and adjustment of practices is essential so that the evidence gained through animal welfare science research can guide best practice and standards. Providing working dogs with positive life experiences (good physical and mental animal welfare) is likely to share the positive consequences observed when farm animal welfare is improved (167). This includes better performance, program efficiency, staff satisfaction, social, and economic benefits. Most importantly, it provides the animals involved with a good life that is worth living. This will be essential for people and dogs to sustain a co-worker relationship that retains social license to operate and respects animal vulnerability in a manner that is not detrimental to the welfare of working dogs.

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MC, CO, and AF contributed to this manuscript's concept and provided content, edits, and review. All authors approved the final manuscript.

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PERSPECTIVE
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The New Era of Canine Science: Reshaping Our Relationships With Dogs

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Canine science is rapidly maturing into an interdisciplinary and highly impactful field with great potential for both basic and translational research. The articles in this *Frontiers* Research Topic, *Our Canine Connection: The History, Benefits and Future of Human-Dog Interactions*, arise from two meetings sponsored by the Wallis Annenberg PetSpace Leadership Institute, which convened experts from diverse areas of canine science to assess the state of the field and challenges and opportunities for its future. In this final *Perspective* paper, we identify a set of overarching themes that will be critical for a productive and sustainable future in canine science. We explore the roles of dog welfare, science communication, and research funding, with an emphasis on developing approaches that benefit people and dogs, alike.

Keywords: canine science, dog, animal welfare, human-animal interaction, science communication, funding, sustainability

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Dogs have played important roles in the lives of humans for millennia (1, 2). However, throughout much of scientific history they have been dismissed as an artificial species with little to contribute to our understanding of the natural world, or our place within it. During the last two decades, this sentiment has changed dramatically; canine science is rapidly maturing into an established, impactful, and highly interdisciplinary field (**Figure 1**). Canine scientists, who previously occupied relatively marginalized roles in academic research, are increasingly being hired at major research universities, and centers devoted to the study of dogs and their interactions with humans are proliferating around the world. The factors underlying dogs' newfound popularity in science are diverse and include (1) increased interest in understanding dog origins, behavior, and cognition; (2) diversification in our approaches to research with non-human animals; (3) recognition of dogs' value as a unique biological model with relevance for humans; and (4) growth in research on the nature and consequences of dog-human interactions, in their myriad forms, from working dog performance to displaced canines living in shelters.

This Perspective represents the final article in a collection of manuscripts arising from two workshops sponsored by the Wallis Annenberg PetSpace Leadership Institute. Leadership Fellows from around the world gathered in 2017 and 2020 to discuss the state of research and future directions in canine science. The individual articles in this collection provide a detailed treatment of key topics discussed at these events. In this final article, we identify a set of overarching challenges that emerge from this work and identify priorities and opportunities for the future of canine science.

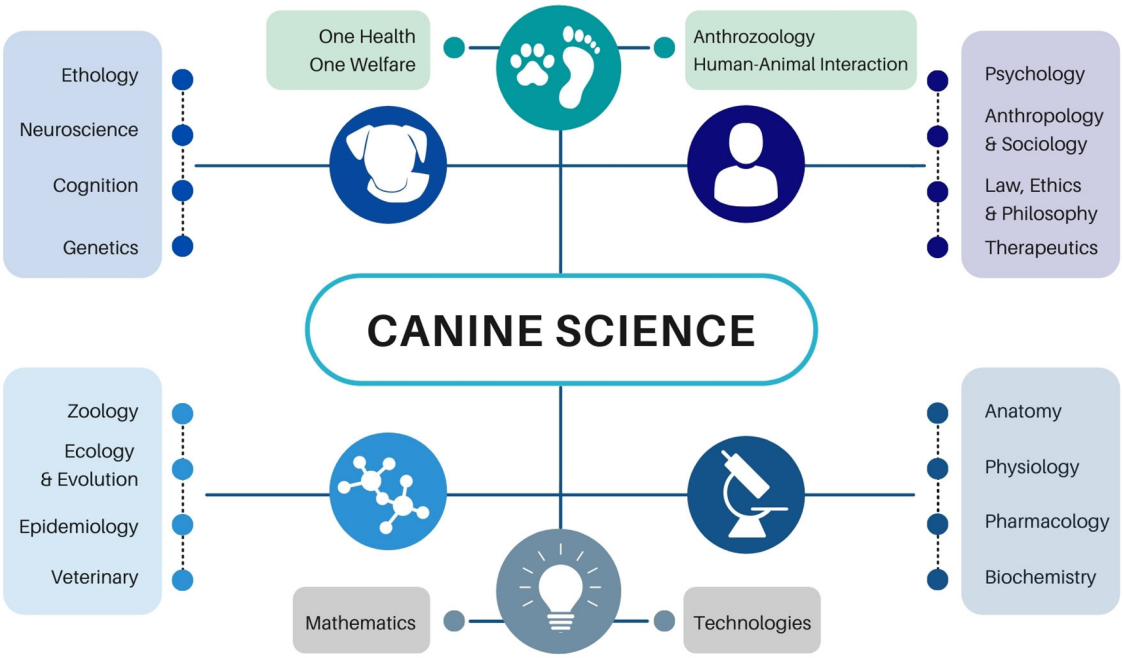

FIGURE 1 | Canine science is an interdisciplinary field with connections to other traditional and emerging areas of research. The specific fields shown overlap in ways not depicted here and are not an exhaustive list of disciplines contributing to canine science. Rather, they are included as examples of the diversity of scholarship in canine science.

The rise of canine science has benefited substantially from public interest and participation in the research process. Unlike many research studies, which unfold quietly in the ivory towers of research universities, the new era of canine science is intentionally public facing. The dogs being studied are not laboratory animals, bred and housed for research purposes, but rather are companions living in private homes, or assisting humans in capacities ranging from assistance for people with disabilities, to medical and explosives detection. Campus-based research laboratories have opened their doors to members of the public who bring their dogs to participate in problem-solving tasks, social interactions, and sometimes even non-invasive neuroimaging studies. Increasingly, dog owners themselves play a significant role in the scientific process, serving as community scientists who contribute to the systematic gathering of data from the convenience of their homes.

This new research model in conjunction with emerging technologies, makes canine science a highly visible field that engages public stakeholders in unprecedented ways. From a scientific perspective, society has become the new laboratory, and in doing so, has facilitated research with dogs of a scope and scale that was heretofore unthinkable. As tens of thousands of dogs contribute to research on topics ranging from cognition and genetics (3, 4) to aging and human loneliness (5), canine science is entering the realm of "big data" and eclipsing many traditional research approaches. Importantly, these advances are occurring simultaneously across diverse fields of science, creating powerful new opportunities for consilience that will make canine science even more valuable in the years ahead. However, maturing this model toward a sustainable future that serves its diverse stakeholders—who include scientists, research funders, members of the public, and dogs themselves—will require careful navigation of key challenges related to dog welfare, science communication, and financial support (**Figure 2**).

DOG WELFARE

Globally, animal welfare has been linked to the public acceptability that underpins sustainable animal interactions and partnerships (6). Where human-animal interactions have failed to meet community expectations, practices and in some case entire industries, have been disrupted or ceased. Recent examples include whaling for profit and greyhound racing (6, 7). Science is not exempt from this necessity to meet with public expectations and the new era of canine science must place canine welfare at the forefront. Considering dogs as individuals and co-workers, rather than tools for work or subjects, reflects a community moral and ethical paradigm shift that is currently underway. Reimagining our relationship with domestic dogs in research will also help inform our treatment of other animals. In this way, studies of dogs and our interactions with them can serve as a pioneering new model for many areas of science.

As scientists advocate for the revision of community and industry practices with dogs in light of new evidence, we must apply the same criteria to the conduct of our research. This

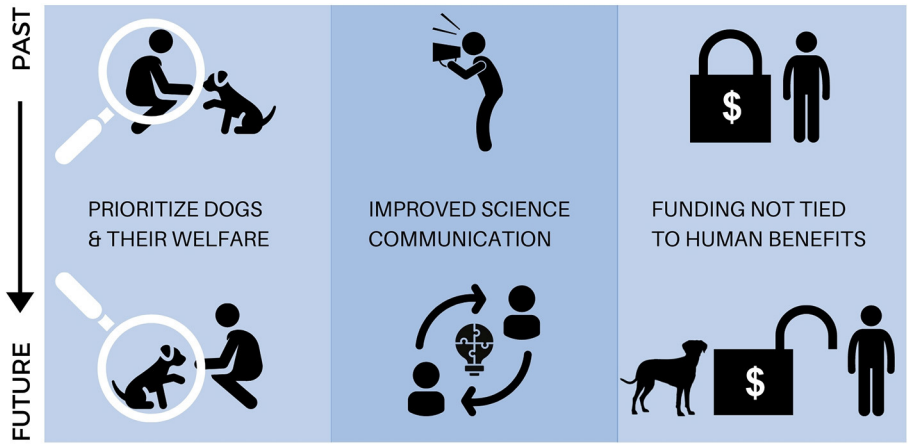

FIGURE 2 | Visual summary of the key issues identified in this *Perspective*. A sustainable future in canine science will require (1) research approaches that prioritize and monitor the welfare of dogs, (2) improved science communication to avoid incorrect reporting of study results, and to translate research findings to meaningful change in practices relating to dogs, and (3) availability of research funding that is not tied exclusively to studying the possible benefits of dogs for humans.

includes adjusting canine research and training methods to acknowledge the sentience of dogs, and the importance of the affective experience for dogs in both research and community settings (8–11). The discipline of animal welfare science has progressed rapidly over the last two decades, and we have many animal-based, welfare-outcome measures available to us (6, 11). Ensuring the well-being of the dogs we study will be as critical to ongoing social license to operate (i.e., community approval) for canine science as it is for working dog interests (12). Being transparent about the issues of animal consent and vulnerability, as well as offering animals agency with regard to their participation in science are valuable suggestions offered within this special issue. We encourage our colleagues to not just consider this paradigm shift, but to effect it through prioritizing and representing the dog's perspective and welfare in their research.

Although increasingly, researchers may include a single or limited set of canine stress measures in studies exploring dogs' potential benefits to humans, this approach alone does not fill the need for studies that prioritize an understanding of canine welfare as their central focus. Canine welfare should be considered not just as an emergent population-level measure (13) but rather with respect to the way in which it is experienced: from the perspectives of individual dogs. Commonly used statistical methods from human research, such as group-based trajectory analysis (14) may offer proven techniques that allow meaningful reporting on populations while reflecting the nuance of shared, sub-group patterns. Such approaches will better reflect individual differences, for example variations in canine personality, social support and relationship styles, as well as other significant factors. One impediment to robust measurement of animal welfare in canine science has been limited funding.

We believe that all granting bodies who fund exploration of the possible benefits to people from dogs should also fund and require the canine perspective to be robustly monitored and reported. Impediments to this work arise not from lack of researcher interest or access to dogs, but rather from challenges to securing funding that is independent from a focus on human health outcomes, or other tangible outcomes of work that dogs perform. To be able to optimize canine welfare, there is an urgent need for increased funding specifically to study the welfare of dogs, in all their diversity. The new era of canine science will identify what dogs need to thrive, propelling us toward a mutually sustainable partnership between people and dogs.

COMMUNICATION

One area that has not received much attention in relation to canine science is the way in which research findings are communicated outside the empirical literature. Fueled by media reports, interest in canine science and the impact of dogs on human health and well-being has grown substantially in the last 10 years. A survey by the Human-Animal Bond Research Institute found that 71% of pet owners were aware of studies demonstrating that pets improve mental and physical health. Some of these claims are justified. For example, many studies have found that interacting with therapy dogs reduces stress and anxiety and increases positive emotional states in a variety of settings including hospitals, schools and nursing homes (15, 16). In other cases, high public expectations about the healing power of pets are not matched by the results of empirical studies. For instance, while the Human-Animal Bond Research Institute survey found that 86% of pet owners believe pets relieve depression, the majority of studies on pet-ownership and depression do not support these conclusions (17).

Because so many people have extensive personal experiences with dogs, investigators face unique challenges in sharing research results with the public. In their hearts, dog owners *believe* that their canine companions make them feel less

depressed, or that dogs feel guilty when they've eliminated indoors or explored the kitchen garbage—even though research might suggest otherwise. In addition, when it comes to animal companions, people much prefer to read a news article in which visits with a therapy dog improved the well-being of a child undergoing chemotherapy than an article about a randomized clinical trial which found no differences between the well-being of children in a therapy dog group and a control group (18). Nor is there likely to be much press coverage devoted to methodological issues such as small effect sizes and inappropriate attributions of causality to the results of correlational studies.

Canine scientists and scholars of human-animal interactions (anthrozoologists) are fortunate that the public is intrinsically interested in our research. We feel that it is critical for investigators to make efforts to communicate the findings of important studies to the public. We caution however, that researchers should not overstate the implications of their findings in press releases and conversations with journalists, despite frequent pressure to do so. These distortions could have a negative impact on misleading the public and misrepresenting the actual findings, a problem that is particularly acute in canine science where well-intentioned pet owners may eagerly adopt practices based on media coverage of scientific studies. The now-established discipline of science communication offers guidance for how best to engage with community and research stakeholders in meaningful ways.

Traditionally, science communication has relied on the knowledge deficit model of communication (19). Directionally one-way, the deficit model operates on the assumption that ignorance is the reason for a lack of community support and application of scientific evidence. Examples where practices have not been updated in response to research findings include dog training methodology (9) and breeding selection for extreme body types, such as brachycephaly in pugs and bulldogs, even though the health and welfare impacts are scientifically well understood (20). Scientists who share their research results thinking that knowledge disseminated—to "educate" the public—is enough to result in different dog care decisions, industry practices or legislation, will generally find this to be ineffective (21). This is because the deficit model overlooks the underlying beliefs, existing attitudes and motivations for current practices. We now recognize that the deficit model is not the most effective way to communicate, engage stakeholders and effect change (22, 23).

Further exploration of the effect of targeted and intentional science communication, informed by human behavior change research, will improve the translation of canine science to meaningful outcomes for dogs and people alike (12). This is important, as many studies in canine science have applied aims designed to inform global policies and the creation of best practices (24, 25). Applied research from the livestock and farming sector suggests that coordinating human behavior change strategies from social and psychological sciences can influence beliefs and attitudes to motivate changes in the ways people behave toward animals, resulting in improved animal welfare (26–28). In the era of attention economics, where scientists are competing for public attention alongside other diverse media, it is vital that the communication of our work is honest, relevant, and effective, to ensure that our field stays on the radar of key stakeholders, funding bodies and change agents.

FUNDING

A third key challenge in the future of canine science concerns research funding and a careful balancing of the priorities of scientists and funding agencies. In the last decade, canine science has received considerable support from the pet care sector, as well as human health and defense agencies [e.g., (29)]. Fine and Andersen (30) stress that although funding is still a challenge in human-animal interaction research, there are now more options to be found. In 2008, the Waltham Petcare Science Institute initiated a public-private partnership with the Eunice Kennedy Shriver National Institute of Child Health and Human Development. Over the past decade, this partnership has provided funding for research aimed at measuring the impact of specific Animal-assisted interventions. Since 2014, the Human Animal Bond Research Institute has funded a total of 35 academic research grants investigating the health outcomes of pet ownership and/or human-animal interaction, both for the people and non-human animals involved. Despite clear benefits for enabling research, there remains a limited group of agencies responsible for funding this work. This has potential to constrain the range of topics being studied. In addition, scientists may feel compelled to support the agendas of industry groups, such as those in the pet sector, who often encourage research that will demonstrate the benefits of pets and human-animal interactions.

These constraints were recognized by Wallis Annenberg PetSpace in 2017 when they envisioned their Leadership Institute Program with a mission to promote interdisciplinary scholarship and convene meetings to accelerate research and policy development (https://www.annenbergpetspace.org/about/leadership). This model for engagement inspired the organization to offer two invited retreats (2017, 2020) for a total of 33 experts in the field that provided opportunities for open ended and frank discussion about the nature of human-animal interaction research, and the maturing field of canine science. By providing the space and financial support, plus the opportunity to work together and publish, Annenberg PetSpace provided a way to both illuminate current limitations, and to identify priorities for the future, free of constraints from outside interest groups. These intellectual salons have no specific agenda other than to consider the future of the field and what kinds of questions need to be asked based on what we already know. The results of these two retreats include 14 published refereed papers, plus a suite of collaborations that might otherwise not have happened. We hope that these fellowships and retreats continue and inspire others to support similar initiatives so that scholars across multiple disciplines have the opportunity to experience the transformational exchanges that occur during these programs. The new era of canine science will require diverse funding that is not limited to how dogs can benefit humans, from health, safety and economic perspectives. This change will enable researchers the freedom to further our understanding of dogs and their needs

for optimized welfare. In turn, this will allow us to identify how dogs and people can thrive together.

LOOKING AHEAD

We hope that the publications emerging from these retreats will reach a diverse community of stakeholders, including students, early career researchers, animal welfare and advocacy groups, legislators and policy makers, philanthropies, and traditional agency funders. The goal of these papers is to spark imagination for projects not yet engaged and to help set the agenda for future research that can enhance our understanding of human-dog interactions and identify paths to ensure a future of symbiotic relationships between these species.

The vision of this collective group of scholars includes the goal of establishing studies with dogs as a sustainable and broad-reaching research focus. Although dogs provide many advantages as a "model species" —including their phenotypic diversity, and shared environments and evolutionary history with humans—a research model centered around dogs has many additional benefits. Dogs provide a rich, interactive and sentient model with deep implications for the way scientists approach animal research, and animal welfare. Dogs also increase the accessibility of research, both literally, due to their ubiquity and opportunities for large-scale public participation in research (31, 32), and figuratively, through a body of work with appeal to the broader public.

The field of canine science has much in common with a similar emerging science, that of urban ecology. Humans are historically at the core of the subject material, but non-human elements are often the focus of the study. As such, the work is always culturally embedded, relevant to a variety of stakeholders, and ultimately expected to improve quality of life. The urban ecologists coined a term *Use-Inspired Research* (33) from modifying the existing idea of Pasteur's Quadrant which organizes research questions across the axes of fundamental understanding and considerations of use (34). Both canine research and urban ecology seek fundamental understanding, but also expect to directly apply the knowledge gained to improve outcomes for their subjects and stakeholders.

By including the public in canine science we not only increase the quantity of the data that we can gather, we serve as ambassadors for a new model of responsible animal research. The result increases the value of human-animal interaction research and creates opportunities for the next generation of interdisciplinary scientists. The goal of this collection has been both to highlight specific recent advances in canine science as well as to identify emerging and overarching issues that will shape the future of this field. The multidisciplinary nature of our work with dogs allows scientists to contribute to a robust research agenda, enhancing our understanding of canines and their impact on society. Ultimately, the nexus of our discoveries should have profound effects on reshaping and enriching our relationships with dogs.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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