A Thesis Presented to

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The Analysis of the Breeding Program for Guiding Eyes for the Blind

by

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Introduction:

When most people think about breeding animals, they typically think about breeding for physical traits and making sure the animals are healthy. Many breeders worry about genetic defects or diseases when choosing which animals to breed and seem to focus more on the physical appearance of the animal rather than how it will behave. This is an issue because deleterious genetic disorders are more likely to occur if reproductive management is not used[22]. Research implies that recessive genetic disorders could be removed from populations in the span of several generations, but only if reproductive management is performed specifically for each genetic disorder[22]. This situation could be more prevalent in pure bred dogs due to a potentially higher risk of inbreeding, which can increase the risk of problems in the offspring.

If these preventative measures—such as genotyping mutations in the dogs that are known to be associated with recessive genetic disorders and examining those mutant allele frequencies in the population—are not taken and breeders continue to only focus on physical traits, then it is likely that the chances of purebreds having recessive genetic disorders will increase[22]. For example, in Border collies, there is a link between congenital sensorineural deafness—a type of deafness present at birth—with the merle gene and phenotypic traits, such as coat pigmentation and iris color[28]. Fortunately, if more precaution was taken to only breed tested and normal parents, the prevalence of this disease could be decreased[28]. Therefore, if breeders focus less on the desired phenotypic traits of the animals and take preventative measures while using reproduction management, they can improve the health of the animals, which is arguably more important than how the animals look. However, it is possible that if breeders focus more on the genetics, and possibly the behavioral traits of animals, instead of their physical features, there could be more improvements and fewer disorders in purebreds. It is better to focus on the health and behavioral aspects of dogs, because the health aspects will influence the quality and length of the dog's life. The behavioral aspects will influence the dog's personality and how it interacts with humans and other dogs. Some research has already started looking into this possibility with several breeds, such as Labrador retrievers, German shepherds, and Border collies. For Border collies, researchers have recently started to consider potentially breeding these dogs to improve their herding traits that used to be more prevalent[32].

Scientists have also used heritability estimates as a way to breed animals more effectively. To put it simply, heritability is the likelihood of traits being passed on from one generation to the next and is the variation in the effects that genetics has on a certain trait[23]. Heritability estimates can be made for both physical and behavioral traits, but this paper will focus mainly on the behavioral aspect. By using heritability estimates to breed animals, animals can be selected to be more sociable and confident, which will increase their level of desirable traits and behaviors. The main goal of this paper is to demonstrate how beneficial it is to use heritability estimates to breed for behavioral traits, and how breeding for behavioral traits could be the next big step for further domestication of tame animals and wild species.

Some breeders have already begun to use these heritability estimates to breed for behavioral traits, and it has been shown to be relatively successful. For example, Guiding Eyes for the Blind (GEB) has been using heritability estimates to breed for desirable behavioral traits in their dogs. Guiding Eyes for the Blind is an organization that breeds, raises, and trains dogs—specifically Labrador retrievers and German shepherds—to become guide dogs for visually impaired people. The dogs that graduate from this organization and its training program help visually impaired people go through their daily lives with more ease and help to keep these people safe.

The method of using heritability estimates for breeding, especially for behavioral traits, is very useful for GEB, because it increases the chances for potential guide dogs to become a phenomenal guide dog to help visually impaired people. These chances increase because behavioral traits, such as dog distraction, noise fear, and harness sensitivity can be selected for by using Estimated Breeding Values (EBVs) (GEB Breeding Manual, 2019, unpublished data; unreferenced). EBVs accurately quantify the genetic merit of the breeding animal and are calculated by accounting for known sources of variation for each phenotypic trait[23]. EBVs also describe how valuable an animal is for breeding, which is based on how likely it is that the animal will pass on a desirable trait to its offspring[21]. When breeders use EBVs as a basis for breeding selection, the genetic gain regarding behavioral traits is likely to increase[21]. Guide dogs make a huge difference to many visually impaired people, allowing them to do more things despite their disability, and these dogs can become even better through the use of heritability estimates for breeding for behavioral traits.

The context for the subject of heritability for this thesis is that Guiding Eyes for the Blind uses heritability measurements and EBVs to decide what traits to apply selective pressure to in order to improve these traits. GEB also uses these measurements to determine the extent to which each trait is connected to genetics, and to determine the extent to which the environment the dogs are raised in impacts the behaviors of these dogs (GEB Breeding Manual, 2019, unpublished data; unreferenced). However, the use of heritability estimates can be and has been used for a long time by other organizations and groups and for many different species, such as livestock and chickens[5].

Background:

The concept of heritability can be traced back to the domestication of wild animals. The domestication of wolves could be viewed as the beginning of applying selection pressures, similar to how GEB uses EBVs to determine what levels of selection pressure to apply to different behavioral traits. However, unlike with the breeding program for GEB, the first steps of the domestication of wolves most likely occurred due to indirect selection of traits by humans. It is unlikely that humans could have directly and intentionally domesticated wolves, because humans used to be extremely afraid of and threatened by wolves. However, vonHoldt et al. have found commonalities in the genetic structure of canine tameness and a disorder characterized by hypersocial behavior[33]. These commonalities could imply that these genetic structures are associated with linked behavioral genes that produce a large phenotypic effect, which could have allowed for the rapid behavioral divergence of dogs and wolves, resulting in the domestication of the wolves[33].

Additionally, it is possible that humans indirectly and unintentionally selected for traits in wolves through their interactions. Wolves may have lurked near human settlements and could have acquired some food from the humans[12]. This could have led to the wolves becoming semi-reliant on humans as a food source. As wolves associated more with humans, they gradually changed their behaviors to be able to peacefully coexist in the same environment. Wolves can adjust their behavior to become more attentive to humans and their body language[12]. For example, Heberlein et al. has found that wolves are more likely to beg for food from humans that are facing them than from humans with their backs turned toward the wolves[12]. This change in behavior could be part of the explanation as to how humans indirectly and semi-accidentally domesticated wolves.

After the apparent accidental domestication of wolves, Belyaev and Trut investigated domestication with foxes[18]. In the famous fox-farm experiment in the second part of the 20th century, Belyaev and Trut selected tame and aggressive foxes (*Vulpes vulpes*) to repeat the process of animal domestication[18]. This experiment focused on behavioral traits that characterized tame versus aggressive behavioral phenotypes, which included the fox wagging its tail, coming to the front of the cage, allowing its head to be touched, and holding the observer's hand with its mouth (without biting the hand). This experiment aimed to determine if these types of behavioral traits could be selected for through the breeding process. In 2008, Kukekova et al. videotaped the foxes to assess their behavior, and in 2011, Kukekova et al. genotyped the foxes to see if there was a significant association between the genes and behavioral traits[18].

From these procedures, this experiment was able to locate a locus—a specific section in a genomic sequence—for tame behavior, as well as a locus relating to active versus passive behaviors on the fox chromosome VVU12[18]. These results imply that there are at least two loci on this chromosome that are associated with behavior, which could mean that there might be more loci on this chromosome or other chromosomes that are associated with behavioral traits. Also, it is interesting that this locus on the fox chromosome is associated with these behavioral traits, because this locus is related to a genomic region on the canine chromosome that has been found to play a role in canine domestication[18]. This relation implies that there might be specific genomic regions, genes, or chromosomes that are associated with behavioral traits in more than one species. It is possible that related chromosomes across multiple species are associated with behavioral traits, and if that is true, then those chromosomes could potentially be manipulated or used during selective breeding for multiple species and could possibly help in the process of domesticating wild species or further domesticating other species, such as dogs.

After the results of the fox farm experiment became more known, organizations that bred and trained service animals began to look at the genetics behind behavioral traits, instead of just physical traits. As science further developed, a way to quantitatively measure the relationship of behavioral traits to genetics was adapted to behavioral traits. This was done by making, interpreting, and applying these estimates to different selective breeding processes used by breeding programs. These heritability estimates could be implemented in their breeding programs as a way to breed for desirable behavioral traits in their animals, which is especially beneficial for breeding programs for service dogs. For example, Guiding Eyes for the Blind (GEB) is an organization that began using heritability estimates to further domesticate and breed dogs for desirable behavioral traits. Specifically, GEB used heritability estimates and estimated breeding values (EBVs) to breed dogs that were more likely to become successful guide dogs.

The purpose of this thesis is to expand the knowledge of heritability and how heritability estimates can be applied to breeding for behavioral traits for multiple species, and to explore the possibility of specific chromosomes being associated with behavioral traits, either cross-species or species-specific. This thesis hypothesizes that Guiding Eyes for the Blind's breeding program is very successful in producing guide dogs with desirable traits, because they use heritability estimates and estimated breeding values to breed for behavioral qualities associated with specific genes.

Section I: Basic Breeding

In the past, breeding has focused on improving the physical traits of animals, and the use of phylogenetic trees has helped to make this possible. Phylogenetic trees are essentially diagrams comparing the relationships of different organisms or groups, and these relationships can be based on genes (Figure 1)[4]. Breeders can use phylogenetic trees to determine what genes—which encode for proteins producing a phenotype—and species consistently produce the same phylogenetic tree over time (indicating shared evolutionary history), and which genes and species evolve in a different way. By identifying these two types of genes, breeders can select for the consistent genes and species to produce offspring with the desired genes and traits. Breeders select for these genes and species because they evolve and reproduce predictably, since they consistently produce the same phylogenetic tree[4]. Phylogenetic trees also show relationships within and among species, and by looking at these relationships, breeders can determine what traits appear to be more heritable for certain animals.

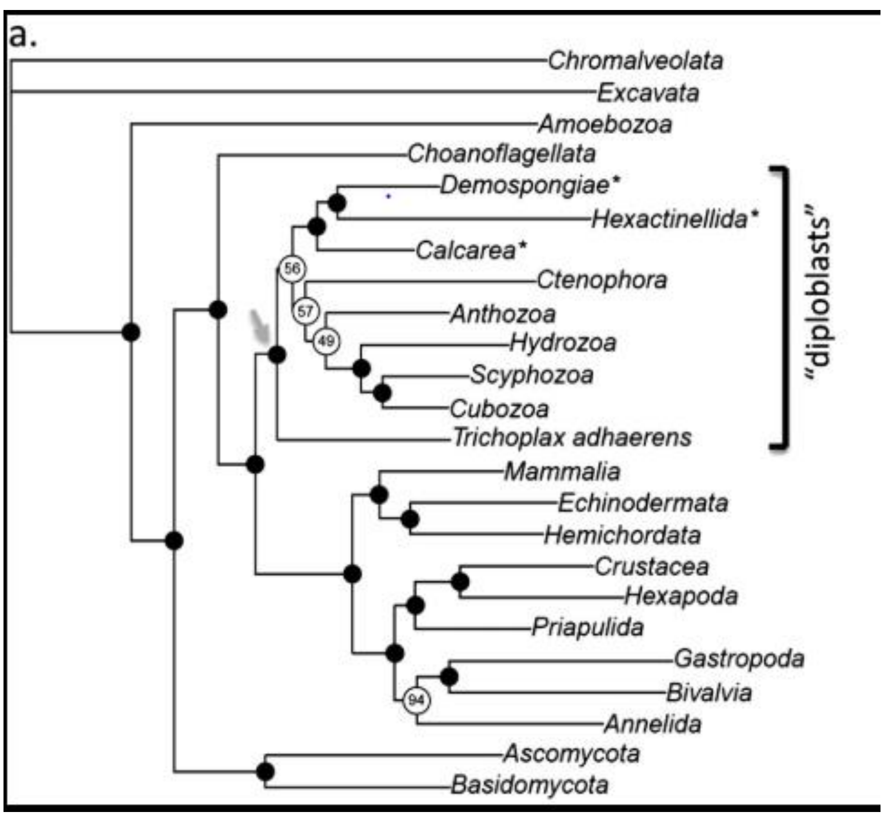

Figure 1. A comparison of the phylogeny of animals from a data set[4].

Once breeders decide what traits they want to see in offspring, they can use a process called selective breeding. Selective breeding is focused selection that exploits genetic variation that is present for most traits with desirable aspects, to improve the genetics of species[9]. Essentially, breeders can apply certain management techniques, such as the use of heritability estimates, to increase the likelihood of desirable genes being passed on to the offspring. It is important for breeders to look at the underlying genes of desirable traits, because genes encode for proteins, and then those proteins determine the phenotype seen in the animal. So, by using phylogenetic trees and selective breeding, breeders can increase their chances of producing offspring that have desirable traits.

Section II: Heritability

I. Breeding for behavioral traits that are linked to genetics

While many breeders select mainly for physical traits, there are other breeders who work to breed for certain desirable behavioral traits, such as sociability, willingness to please, trainability, nerve stability, hardness, sharpness, and courage. Sociability can be described as the behavior of animals toward and interactions with humans[26]. More specifically, it refers to how friendly and social animals are to humans, as well as their willingness to be social and interact[20]. Willingness to please can be described as how willing the animal is to make its trainer happy by doing what the trainer instructs. Trainability is how easily and how well the animal attends to and obeys the trainer. An animal with high trainability does not get distracted easily, is a fast learner, and positively responds to correction[20]. Nerve stability refers to how appropriately an animal reacts and adapts to various situations[21, 35]. Animals with high nerve stability are not easily frightened, nervous, or extremely sensitive, and are able to concentrate and relax in unpleasant situations. Hardness is the ability of the animal to not have a lasting effect from pleasant or unpleasant situations. Sharpness is the tendency of the animal to react with aggression in potentially threatening situations. The desirable aspect of this trait is for the animal to show aggressive behavior—but not from fear—when it or the handler is threatened, but then to stop the aggression quickly once the threat is gone[21, 35]. Courage is the ability of the animal to overcome fear[35]. These behavioral traits are desirable for animals to have, and several, if not all, of them can be selected for through selective breeding.

There are different methods that breeders can use to select for desirable behavioral traits both before and after the birth of the offspring. Once the offspring are born, no genetic change can be done, but different training methods or programs can be used to encourage the display of desirable behavioral traits, as well as enhance desired characteristics. For example, research has shown that the use of structured breeding programs can further enhance the desired working characteristics of service dogs[36]. These goal-oriented breeding programs focus on certain desirable characteristics, such as mental stability and willingness to please, which can help improve the behaviors of dogs bred through these programs[36]. These programs are important to have for any breeder who wants to see specific behaviors in their animals but are especially important for raising and training working animals, such as service dogs. However, while these structured breeding programs are helpful to improve certain desirable characteristics, these desirable behaviors are more likely to be displayed and passed on through the generations if selection pressures are applied prior to breeding.

During the breeding process and prior to the birth of offspring, many breeders apply some kind of selection pressure(s). Some use index values calculated from a factor analysis of a few select desirable characteristics[36]. In these cases, breeders can choose to only breed animals whose litters had a higher than average mean index value[36]. By doing so, only the animals with the best characteristics are bred, with the hope that breeding the most desirable animals will result in offspring with similar levels of desirable characteristics. This hope is based on the idea that these characteristics can be inherited, which would mean these characteristics are somehow associated with genetics. Similar to using index values, other breeders may use breeding values to apply selection pressure[21]. Breeding values, calculated from scores for traits based on a numerical scale, describe how valuable an animal is for breeding based on how likely it is that the animal will pass on a desirable trait to its offspring. If breeders use breeding values as a basis for selection for breeding, then it is likely that the phenotypic gain regarding characteristics, such as desirable behavioral traits, will increase[21]. However, the effectiveness and success of the use of these values to increase the occurrence of desirable traits depends on whether or not the traits are heritable.

Fortunately, based on observed genetic trends, studies have found that by using these methods of selective breeding, certain desirable traits improved over time, which indicates that there is, in fact, a genetic basis for certain behavioral traits[21, 35]. Additionally, many studies have been able to associate specific chromosomal regions and specific loci with certain behavioral traits. For example, vonHoldt et al. found chromosomal regions and specific loci that can be connected to extreme sociability in dogs[33]. This extreme sociability is called hypersociability and has been associated with genes within the Williams-Beuren syndrome (WBS) locus. WBS is present in humans as well, and it is characterized by hyper-social behavior, which is desirable for dogs, because hypersocial dogs are more likely to initiate social contact with other species via extended proximity seeking and gaze, as well as they become more dependent on humans to solve problems. Fortunately for breeders, hypersociability is a heritable behavioral trait[33]. This conclusion of heritability is based on the findings that structural variants in GTF21 and GTF21RD1—a set of paralogous genes[33] (homologous genes that evolved from an ancestral gene, duplicated, then diverged)[17] that are members of the transcription factor II-I (TFII-I) family that regulate vertebrate development—are significantly associated with hypersociability in dogs[33]. This strong connection between this behavior and specific genes provides breeders with information about what behavioral traits they could potentially breed for if they use selective breeding based on genetics.

In addition to GTF21 and GTF21RD1, other genomic regions have been found to be associated with human-directed social behavior[16, 33]. The association between behavior and genomic regions can provide more genetic information to breeders to use to estimate the heritability of behavioral traits. One of the other genes associated with human-directed social behavior is the oxytocin receptor gene. Oxytocin receptor gene polymorphisms have an impact on more than one dog breed, regarding proximity seeking toward a human and friendliness toward strangers[16, 33]. More specifically, three single nucleotide polymorphisms (SNPs) in the dog oxytocin receptor gene in German shepherds and Border collies—rs8679684, 19131AG, and -212AG—were found to be significantly associated with these behaviors[16]. Polymorphisms are variations in the alleles in a genetic sequence, while a SNP is the occurrence of two or more alleles at a specific chromosome location[37]. The proximity seeking trait was associated with the -212AG polymorphism, while the friendliness trait was associated with the other two polymorphisms (refer to Table 1)[16]. These associations between the polymorphisms of the oxytocin receptor gene and behavioral traits indicate that the oxytocin system does influence the social behavior of dogs toward humans[16]. This is beneficial for breeders, because it suggests the possibility of being able to breed for this gene to increase the heritability estimates of this trait, thereby increasing the chances of offspring inheriting this desirable trait of sociability.

Table 1. Associations of the oxytocin receptor gene single nucleotide polymorphisms with the behavioral traits[16].

	German Shepherds			Border Collies		
Oxytocin receptor gene SNPs	-212AG	rs8679684	19131AG	-212AG	rs8679684	19131AG
Proximity seeking	F=4.030*	t=0.641 ns.	t=0.931 ns.	t=2.282*	t=1.119 ns.	t=0.964 ns.
Reaction to separation from owner	F=1.083 ns.	t=0.096 ns.	t=0.147 ns.	t=1.581 ns.	t=0.738 ns.	t=0.473 ns.
Friendliness	F=0.171 ns.	t=2.570*	t=2.724**	t=0.739 ns.	t=2.412*	t=2.800*
Looking at humans	F=0.710 ns.	t=0.140 ns.	t=0.022 ns.	t=1.514 ns.	t=1.242 ns.	t=1.514 ns.

**: p<0.01
*: p<0.05
ns: p>0.05

Other genomic regions associated with human-directed social behavior can be found on canine chromosome 26. A total of three genetic markers (identified loci) have been found to be strongly associated with this desirable behavioral trait, and some of these have been found for beagles and for golden and Labrador retrievers. For beagles, three SNPs (found through genotyping the dogs) on chromosome 26 were associated with sociable behavior: BICF2G630798942, BICF2S23712115, and BICF2S23712114[27]. The SNP BICF2G630798942 located within the SEZ6L gene was significantly associated with two types of human-directed social behavior: duration of close proximity to humans and duration of seeking physical contact with humans. The other two SNPs within the ARVCF gene on chromosome 26, BICF2S23712115 and BICF2S23712114, were only associated (just short of significantly associated) with the duration of seeking human physical contact[27]. Similar to these SNPs in beagles, two of the same SNPs on chromosome 26 were found to be associated with human-directed social behavior for golden and Labrador retrievers[26]. The two SNPs that are associated with this behavior in golden and Labrador retrievers are BICF2G630798942 and BICF2S23712114, which infers that these specific genomic regions are associated with human-directed social behavior in more than one dog breed[26]. These genomic regions were also probably under strong selection pressures for sociability and were probably affected by domestication, so breeders could potentially use information about these genes to help decide which animals to breed, which could help improve the heritability estimates of these desirable behavioral traits. Interestingly enough, in humans, the SEZ6L gene has recently been linked with the autism spectrum disorder, which can impair social interactions and communication[27]. The ARVCF gene, on the other hand, has been associated with schizophrenia[27]. If the connection between these genes and these disorders—autism and schizophrenia—is also present in animals, that could help explain why polymorphisms in these genes affect the sociability of dogs, because both disorders affect the behavior of organisms, especially in social situations. These results all indicate that there is a genetic basis for some human-directed social behavior in dogs.

Fortunately, breeders are not limited to only breeding for sociability in terms of heritable behaviors, because other studies have found other behavioral traits that are influenced by genomic regions, which are sections in a genomic sequence. Specifically, eleven SNPs (in eight genomic regions) were inferred to be associated with six behavioral traits as follows: agitated when ignored associated with BICF2P964118 on chromosome 18; barking tendency associated with BICF2P696817 on chromosome 4; fetching associated with BICF2G630792579 on chromosome 1, with BICF2P844921, BICF2P456276, BICF2P73495, and BICF2P519369 on chromosome 4, and with BICF2S2314224 on chromosome 22; noise fear associated with BICF2P846231 on chromosome 20, non-owner-directed aggression associated with BICF2G630832223 on chromosome 9, and unusual behavior associated with BICF2P612229 on chromosome 2[13]. The largest effects of SNPs on behaviors were for fetching and noise fear. However, despite these results from the genomic analyses of these traits that infer that there are chromosomal associations for these six behavioral traits, most of the behavioral traits examined in the same study are polygenic, which means that individual genomic regions only have small effects[13].

Overall, there have been several studies that have provided evidence that behavioral traits can be connected to genetics and chromosomal regions, which allows breeders to look at the genetics of desirable behavioral traits that they want to select for (Table 2). Breeders can interpret and take advantage of these associations between the genetics and behavioral traits by using heritability and marker-assisted selection. Marker-assisted selection (MAS) involves using genetic markers with consistent trait association to determine which animals would be the best to use for breeding to improve the average rate of trait improvement from generation to generation[34].

II. Defining heritability

Heritability can play a very important role in breeding, both for behavioral and physical traits, and the term heritability has been defined in a few different ways. Guiding Eyes for the Blind defines heritability as “the degree to which genes cause the phenotype that can be measured” (GEB Breeding Manual, 2019, unpublished data; unreferenced). This means that if the heritability is higher, then selection can improve the selected trait more and at a faster rate

(GEB Breeding Manual, 2019, unpublished data; unreferenced). Other sources have defined heritability as "the proportion of the total variance that is attributable to the average effects of genes"[6] or "the ratio of additive genetic variance to phenotypic value"[6]. More specifically, there is a difference between broad-sense heritability (H^2) and narrow-sense heritability (h^2). Broad-sense heritability includes dominance in relationships between genes, but narrow-sense heritability does not include dominance. Instead, narrow-sense heritability "estimates the additive genetic contribution to a phenotypic trait"[25] and focuses on one type of interaction at a time, such as a dog's social skills. Narrow-sense heritability looks at which alleles contribute more to the trait than other alleles. Narrow-sense heritability has been investigated in several behaviors such as hunting behavior, working performance, aggression, and some social skills[25]. The type of heritability that will be addressed for this thesis is narrow-sense heritability and will be defined as the ratio of how much of an effect the genotype has on the phenotype—behavior in this case—of the organism.

III. Interpreting heritability estimates

An important aspect of heritability is that quantitative heritability estimates can take additive genetic variance into account[6]. Heritability estimates are denoted as numbers between zero and one, because they represent a ratio of the genetic contribution to phenotype to all factors. Based on the numerical values placed on these heritabilities, breeders can determine which traits are better options to use for selective breeding: the traits with higher heritability estimates, which are closer to one. Conversely, the traits that have lower heritability have estimates that are closer to zero, and these traits most likely will not have a strong association with genetics (GEB Breeding Manual, 2019, unpublished data; unreferenced)[6]. Variations in the occurrence and prevalence of consistent behavioral traits implies that the environmental aspect does have a large impact on the heritability aspect of these behaviors, but it can change from generation to generation.

Even though these variable heritability estimates can be applied to breeding to predict behaviors, the numerical range of heritability estimates indicating a higher heritability is relative to each population. For example, human-directed social behavior has a heritability estimate of 0.23 in dogs, and that trait is considered to have a strong association with genetics[25]. Similarly, other studies have found the more heritable behavioral traits to have heritability estimates with a range from about 0.20 to 0.40[13, 21, 30, 36]. For these behavioral traits, the heritability estimates that are considered high are typically relative to the heritability estimates that are much lower within the same experiment. However, even the behavioral traits that are considered to have high heritability estimates are still influenced by environmental factors, such as how the animal is raised and trained. So, while heritability estimates above 0.20 seem to be considered highly heritable for behavioral traits, it is important to remember that there are other factors, such as environmental factors, that have an impact on the heritability of a trait.

IV. The reliability of using heritability for breeding for desirable traits

While higher heritability estimates can be used to effectively predict behaviors in subsequent breeding, it is important to remember that all genetic components are affected by gene frequencies, so heritability estimates can change from population to population[6]. These differences between populations are because of environmental variance, such as differences in conditions. More variable conditions reduce the heritability of traits, while more uniform conditions increase the heritability[6]. Essentially, even though higher heritability estimates can be used to effectively predict behaviors in subsequent breeding, there are still other factors that can decrease the influence of heritability for breeding animals for desirable traits.

Regarding Guiding Eyes for the Blind, if a trait has a high heritability value, selection pressure is applied, Estimated Breeding Values (EBVs) are used, and results from the breeding program have shown a positive result (GEB Breeding Manual, 2019, unpublished data; unreferenced). This implies that the use of heritability estimates and EBVs for the breeding program for Guiding Eyes for the Blind is a reliable way to predict behaviors in subsequent breeding in this program.

Section III: Guiding Eyes for the Blind (GEB)

I. How GEB uses heritability

Guiding Eyes for the Blind (GEB) breeds, raises, and trains guide dogs for visually impaired people. In this line of work, it is very important for these dogs to have the best possible genetics, both physically and behaviorally, because it is important for these dogs to be healthy and have desirable behavioral traits in order to become successful guide dogs. The breeding program for GEB measures and uses heritability estimates to help improve the physical and behavioral traits of these potential guide dogs (GEB Breeding Manual, 2019, unpublished data; unreferenced). Heritability estimates help breeders determine if the trait will respond to genetic selection and to what extent[36]. If the heritability estimate is closer to one, then the trait is more likely to respond to genetic selection, but if it is closer to zero, then the trait is probably more impacted by the environment and will not respond as much to genetic selection[36].

Additionally, the breeders for GEB can use heritability estimates to determine how they select for each trait or phenotype. GEB wants to breed dogs with the most ideal traits both physically and behaviorally, so they rely on the heritability estimates of traits to determine what dogs they breed and what traits they breed for each time. They will most likely apply more selective pressure to traits that are more heritable. The use of estimated breeding values (EBVs) is also an option for breeders to use to determine which dogs would be the most beneficial to breed. Guiding Eyes for the Blind also decides what traits to breed for based on traits that are common reasons for a dog to be dismissed from the guide program. In order for this kind of selection to be effective, this selection process needs to be practiced consistently for a few traits over several generations[34]. Consistently using the same selection criteria for several generations will result in the increase of gene frequency of the specific desired traits and the decrease of gene frequency of the undesirable traits. This then results in a larger percentage of offspring that have and display the desirable genes and the associated desirable traits[34].

II. Physical traits GEB considers

In terms of physical traits or potential issues, Guiding Eyes for the Blind (GEB) breeds for and against certain physical traits using heritability estimates and by genotyping. The dogs are genotyped prior to breeding for diseases that have genetic tests and that are a possible risk to the GEB population/colony (GEB, 2019, unpublished data; unreferenced). This type of selective breeding can be described as marker assisted selection, which was defined in Section II[34]. In this case, the genetic markers used are associated with certain diseases that could affect the GEB population. Some of the physical traits that GEB selects against include elbow dysplasia, epileptic seizures, atopic dermatitis, and tricuspid valve dysplasia (GEB Breeding Manual, 2019, unpublished data; unreferenced). Elbow dysplasia is a progressive skeletal disease that can cause lameness, pain when the affected limb moves, and secondary osteoarthritic changes such as osteophytes or primary lesions[14]. A dog with this disease would not be a good potential guide dog. The main job of a guide dog is to lead its visually impaired person and keep that person safe, and that would be much harder if the dog is lame or in pain whenever it walks. Fortunately, the heritability estimate for elbow dysplasia has a range from 0.68 to 0.98, for a study done with German shepherds[15]. This high heritability estimate suggests that by breeding dogs that are unaffected by this disease, the chances of these dogs developing this disease will be lower[15]. Therefore, by using heritability estimates of this disease, breeders for Guiding Eyes for the Blind can successfully apply selection pressures to decrease the prevalence of this disease in their dogs.

Similar to elbow dysplasia, the heritability estimates for epileptic seizures are also very high: 0.77 for Belgian tervuerens[7] and 0.87 for Irish wolfhounds[2]. These high estimates suggest an association with a major gene, and it means that breeders can use selective breeding to decrease the incidence of epileptic seizures. It is important the dogs bred for Guiding Eyes for the Blind do not have this disorder, because epileptic seizures can be defined as occasional, sudden events that are associated with electrical and behavioral changes in the brain[3]. This disorder would be detrimental to guide dog work, because successful guide dogs need to stay sharp and aware at all times. If a guide dog had an epileptic seizure while guiding a visually impaired person, that could put the person in danger, because the dog may become unaware of potential dangers.

Another physical trait that has been found to have high heritability estimates is tricuspid valve dysplasia. Tricuspid valve dysplasia is a range of congenital malformations of the tricuspid valve apparatus in the heart[24]. Some of these malformations are “focal or diffuse thickening of the leaflets, underdevelopment or undifferentiated chordae tendineae (CT) and papillary muscles (PM), incomplete separation of valve components from the ventricular wall, and focal agenesis of valvular tissue"[24] (Figure 2). This disease has been found to be a heritable disorder in Labrador retrievers, so dogs with this disorder or dogs closely related to the affected dogs should not be used for breeding[24]. This is an important factor to consider especially for Guiding Eyes for the Blind (GEB), because a large majority of the dogs bred and trained are Labrador retrievers. Fortunately, the heritability estimate of tricuspid valve dysplasia has been found to be 0.71[8]. Therefore, the breeders have a better chance of being able to successfully select against this disorder by choosing to not breed dogs that have this disorder or have family members with this order.

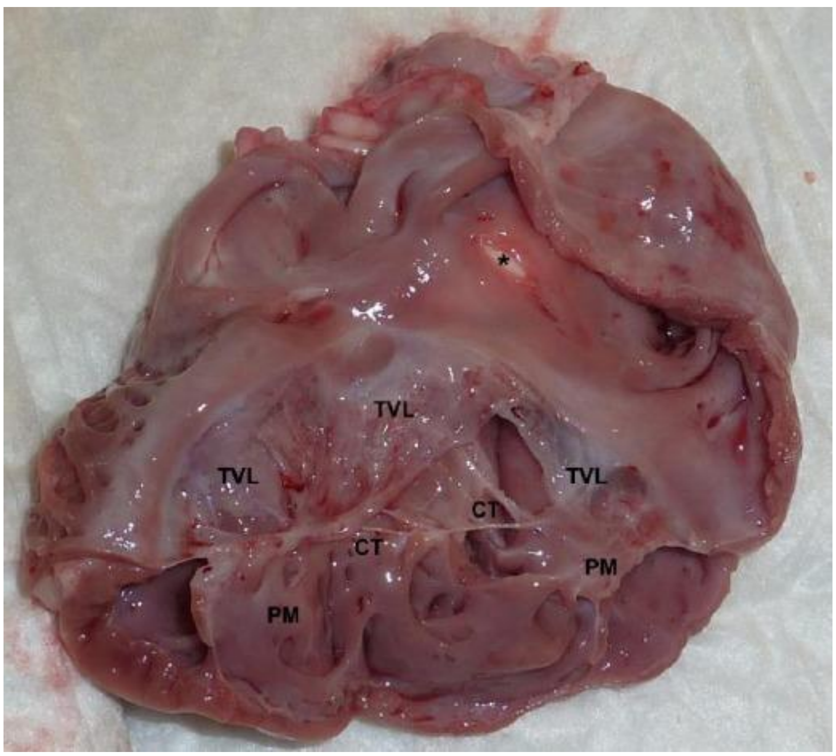

Figure 2. A post-mortem image of the heart from a 3-month old Labrador retriever puppy diagnosed with tricuspid valve dysplasia. The tricuspid leaflets exhibit diffuse marked thickening and the right atrium is enlarged. Also, the chordae tendineae and papillary muscles are shortened, fused, and thickened[24].

Finally, out of these physical traits studied, atopic dermatitis has the lowest heritability estimate of 0.47, as was found in a study about Labrador and golden retrievers[31]. However, atopic dermatitis is still considered to be heritable, and to have a strong genetic component. So, it is important for Guiding Eyes for the Blind, and other breeders, to avoid breeding dogs that show clinical signs of atopic dermatitis[31]. This disease is characterized by lesions, immunoglobulin E sensitization to common environmental allergen sources, and epidermal barrier dysfunction[11]. This disease would be undesirable for service dogs, because it is important for the dogs to be healthy to help their humans. Additionally, guide dogs will need to wear harnesses to guide their visually impaired humans and having skin conditions could negatively affect how well they work with the harnesses on. If the harnesses are constantly rubbing against their sensitive skin, then the dogs are more likely to become distracted, which could be very dangerous for the visually impaired person that they are guiding.

Studies have shown that all of these traits have relatively high heritability estimates, which suggests that they are strongly associated with specific genes. This is beneficial to breeding for Guiding Eyes for the Blind (GEB), because it allows GEB to select against certain physical traits that they find undesirable in their guide dogs. However, in addition to selecting against these physical disorders or diseases, GEB also uses heritability estimates to select for certain behavioral traits, such as confidence, distraction (human and dog), ease of handling, personality (shyness-boldness), noise fear, and harness sensitivity (GEB Breeding Manual, 2019, unpublished data; unreferenced). The behavioral traits of guide dogs for Guiding Eyes for the Blind is very important, because there are several desirable behaviors for a guide dog to be the most ideal guide dog.

III. Behavioral traits GEB considers

Guiding Eyes for the Blind defines confidence, distraction, and ease of handling as three components to determine the temperament and overall trainability of a guide dog in training (GEB Breeding Manual, 2019, unpublished data; unreferenced). Other studies have defined (self-) confidence as how assertive the dog is in different situations[21]. High self-confidence would be characterized by dogs who remained calm without being afraid, attentive without worrying, and remained friendly[21]. High confidence is desirable for guide dogs, because it will allow them to stay attentive to the visually impaired person that they are guiding in any situation, while remaining calm. This trait will allow the guide dogs to keep the human safe, which is one of the components that makes a guide dog successful. Additionally, Guiding Eyes for the Blind defines temperament as being comprised of the dog's confidence, distraction, and ease-of-handling (GEB Breeding Manual, 2019, unpublished data; unreferenced). However, other studies have defined temperament as "an intense interest in all objects [that] is expressed in physical activity"[21] or the level of liveliness and responsiveness[35]. These definitions are not very similar, so the data and heritability estimates may have different meanings and interpretations for these two cases, regarding the dogs' behavior.

Additionally, personality has been described by Guiding Eyes for the blind as the difference between shyness and boldness (GEB Breeding Manual, 2019, unpublished data; unreferenced). Other studies have described personality as a collection of how the dog responds to different situations, such as social contact, play, chase, and metallic noise. Saetre et al. found the heritability estimate for personality to be 0.25[30]. This estimate is much lower than the heritability estimates for the physical traits, but when compared with other behavioral traits, it is relatively high.

The last two behavioral traits that Guiding Eyes for the Blind (GEB) considers when breeding is harness sensitivity, which describes how drastically the dogs respond to wearing a harness, and noise fear, which describes how a dog reacts to loud noises (GEB Breeding Manual, 2019, unpublished data; unreferenced). Other studies have focused more specifically on reaction to gunfire, but both behaviors focus on the reaction of the dog in response to loud and potentially unexpected noises. The desirable behavior regarding noise fear is that the dog will potentially react to the loud noise, but not be afraid of the noise[21, 35]. Overall, there are several behavioral traits that Guiding Eyes for the Blind selects for during the breeding process, but there are different levels of success when it comes to seeing these desirable behaviors being passed on to the offspring (Table 3).

While Guiding Eyes for the Blind (GEB) does not specifically use marker assisted selection to breed for behavioral traits, GEB does use estimated breeding values (EBVs) to select what dogs to breed. GEB collects data from all related dogs and runs that data through a program set up to get the list of EBV numbers. GEB also observes the variation in behavior and looks at the data from each dog and its relatives to calculate heritability estimates for the behavioral traits of each dog (GEB, 2019, unpublished data; unreferenced). Finally, GEB uses phenotypic selection, which is when individuals are chosen for breeding based on their observed and measured phenotypic traits[34].

IV. Heritability of behavioral traits for GEB dogs

One of the behavioral traits that Guiding Eyes for the Blind breeds for is dog distraction. Unfortunately, the heritability estimate for this trait is very low at 0.06, so selection will not be able to do much to improve the expression of this behavior over time. Due to the low heritability estimate, Guiding Eyes for the Blind uses behavior checklist data to identify dogs at risk of having high dog distraction. Also, since there is very little genetic association with this trait, the environment has a larger impact on this trait (see Figure 3) (GEB, 2019, unpublished data; unreferenced). Even though the low heritability estimate means any improvement of this trait due to genetic selection is limited, Guiding Eyes for the Blind still selects for this trait, because it is such an important behavioral trait to possess for guide dogs.

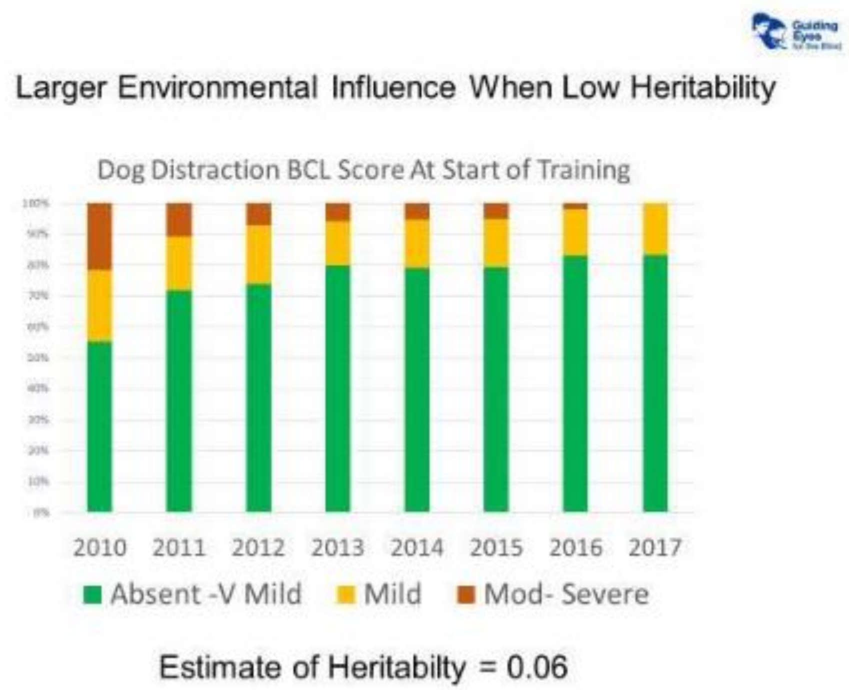

Figure 3. The comparisons of dog distraction according to the Behavior Checklist scoring system (BCL) over the course of eight years, and the calculated heritability estimate for dog distraction for dogs bred through Guiding Eyes for the Blind (GEB, 2019, unpublished data; unreferenced).

Another behavioral trait that Guiding Eyes for the Blind (GEB) selects for is noise fear. The heritability estimate of noise fear for GEB is 0.26, which is still not very heritable, but it is more heritable than dog distraction (GEB, 2019, unpublished data; unreferenced). Guiding Eyes for the Blind has made progress over the years to improve this trait in dogs through running Estimated Breeding Values (EBVs) and applying selection pressure to this trait (GEB Breeding Manual, 2019, unpublished data; unreferenced). This improvement can be seen in the breeding program of Guiding Eyes for the Blind, because from 2010 to 2016, GEB has been successful in decreasing the proportion of severe and moderate noise fear in dogs from 9.5 percent to 6.6 percent in the population (Figure 4) (GEB, 2019, unpublished data; unreferenced). Figure 4 shows that there are fluctuations in the proportion of different levels of noise sensitivity over the years. However, the more extreme cases of noise sensitivity have decreased over time and have been replaced with more mild or absent occurrences of noise sensitivity. This data infers that by using the heritability estimates of traits to decide what traits to apply selection pressure to, breeders can improve the behavioral traits of the animals they are breeding.

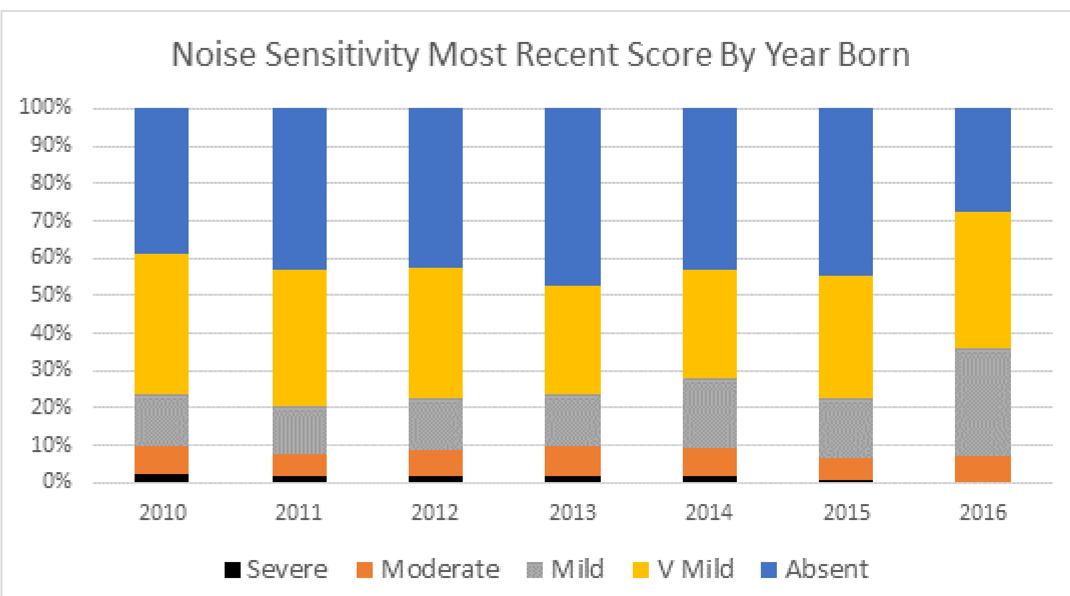

Figure 4. The comparison of levels of noise sensitivity from 2010 to 2016 in dogs bred through Guiding Eyes for the Blind (GEB, 2019, unpublished data; unreferenced).

The final behavioral trait to be discussed that Guiding Eyes for the Blind breeds for is harness sensitivity, and it is the most heritable out of the three behaviors. The heritability estimate for this behavior is 0.36, and it is actively selected for by using EBVs. From 2012 to 2016, Guiding Eyes for the Blind has been able to improve this trait, and the severe and moderate harness sensitivity incidences decreased from 13.1 percent to 6.6 percent, which is a 50 percent decrease in the two generations of selection (Figure 5). Additionally, the percentage of harness sensitivity being absent from the GEB population increased from above 50 percent to above 60 percent of the population from 2010 to 2016. This data shows that genetic selection can play a large role in improving this behavioral trait (GEB, 2019, unpublished data; unreferenced). These applications of heritability estimates and EBVs during breeding, show that heritability estimates can be used for many species to breed for desirable behavioral qualities.

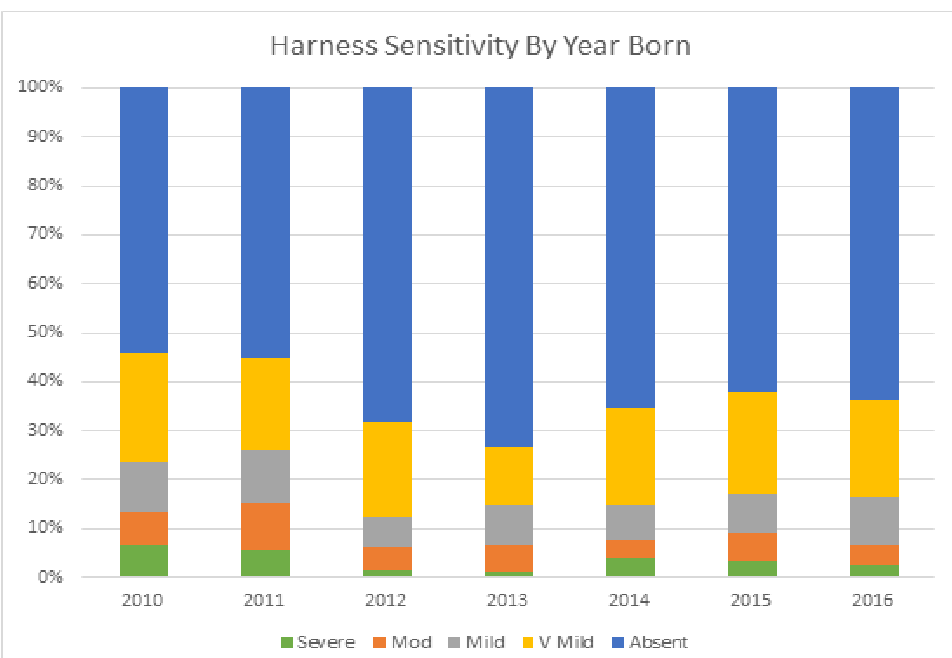

Figure 5. The comparison of levels of harness sensitivity from 2010 to 2016 in dogs that are bred through Guiding Eyes for the Blind (GEB, 2019, unpublished data; unreferenced).

V. Predictability of behavioral traits for GEB

Among the three traits discussed for the breeding program for Guiding Eyes for the Blind, dog distraction was the least predictable, because the heritability estimate was so low (0.06) (GEB, 2019, unpublished data; unreferenced). Heritability estimates can not reliably be used to predict behaviors in subsequent breeding unless they are considered to be high[36]. However, the heritability estimate of noise fear (0.26) is high enough where it can be used to more reliably predict behaviors in future offspring. In addition to the higher heritability, the use of Estimated Breeding Values (EBVs), which increased as time passed from one generation to the next (Figure 4) and applying selection pressure helped cause the proportion of severe and moderate noise fear to drop from 9.5 percent to 6.6 percent in six years. Since the heritability estimate of harness sensitivity (0.36) was the highest, it is relatively reliable to correctly predict the behaviors of subsequent offspring. In addition to using the heritability estimates, applying selection pressure through the use of EBVs helped to decrease the cases of severe and moderate harness sensitivity by 50 percent within two generations of selection (GEB, 2019, unpublished data; unreferenced).

VI. Environmental effects

Finally, the effect of the environment on these behavioral traits varied, depending on how low or high the heritability estimates were. Because the heritability estimate for dog distraction was very low, this trait can be expected to be greatly affected by the environment. Low heritability typically means that the environmental influence is larger, because the genetic influence is much smaller and more limited. The heritability estimate of noise fear was higher than that of dog distraction, but it is still not extremely high, so this behavioral trait is probably semi-affected by the environment and how the dog is raised and trained. However, there is a decent genetic aspect to this trait, so the environment does not entirely control the outcome of this behavior. Finally, the heritability estimate of harness sensitivity is relatively high, so there is a large genetic influence for this behavior, but there is also an environmental impact, such as training within the Guiding Eyes for the Blind program (GEB, 2019, unpublished data; unreferenced).

Since the environment does have a relatively large impact on behavioral traits, Guiding Eyes for the Blind (GEB) employs a few methods to decrease any negative impact that the environment could have. One method is by having a strict set of rules for every GEB volunteer (mainly raisers and sitters) to follow. The rules the dogs must follow remains consistent, which can help improve or reinforce good behavior. Also, the verbal and nonverbal cues for all commands remains the same, which adds to the consistency. Finally, every dog in training has periodic sessions with a GEB staff member throughout its time with its raiser to ensure that each dog is on track and is doing what it is supposed to do.

Overall, Guiding Eyes for the Blind (GEB) has a lot of physical and behavioral traits to consider when breeding its dogs, but this breeding program has been able to use heritability estimates to improve the prevalence of these desirable traits over time. Guiding Eyes for the Blind could probably breed its dogs without using heritability estimates, but the data discussed would infer that GEB will be more successful in breeding for desirable behavioral traits if it uses heritability estimates and applies selection pressure through the use of Estimated Breeding Values.

<u>Section IV. Other experiments focusing on behavioral traits</u>

Even though breeding for behavioral traits is very important for training guide dogs or service dogs, there are a couple other main reasons to breed for behavioral traits. First, there are many different jobs for working dogs besides guide work or service work. Some dogs are trained to become police dogs, security dogs, bomb or drug detector dogs, and other kinds of work. These job types also typically require these working dogs to have special abilities and behaviors. For example, it can be inferred that dogs who are trained to detect drugs need to have a heightened sense of smell, as well as the ability to differentiate between scents of substances that are illegal and legal. Additionally, canine units typically have a greater need to be aggressive in order to deal with potential threats or dangerous situations. Meyer et al. found that using heritability to breed for this behavioral trait could be a possibility, albeit a small one[21]. The aggressive behavior that canine units would benefit from inheriting has been labeled as sharpness. Sharpness describes how aggressively the dog reacts to a potentially threatening situation. The desirable behavior is that the dog shows aggressive behavior, but not from fear, when the dog or handler is threatened, but that aggression should stop quickly once the threat is no longer present. This behavioral trait had a heritability estimate of 0.06 for German shepherds, so it may not have a strong genetic correlation currently[21]. However, it is possible that over time, breeders could select for this trait, which could increase its prevalence and potentially improve its heritability estimate. If this is possible, it can be inferred that that would be helpful for programs such as the canine unit for police departments. If this behavioral trait could be bred for, it could help the dogs in canine units to protect themselves and their handlers from criminals and potentially dangerous people.

The other major reason for people to breed for behavioral traits is for the purposes of domestication and making animals more sociable. This domestication incentive is applicable for dogs and other species, including wild animals. Domestication is associated with various behavioral characteristics, and it is necessary to analyze both behavioral and genetic data to fully understand how these characteristics develop[33]. So, the use of heritability estimates to further the domestication of multiple species is a useful method.

Besides Guiding Eyes for the Blind, there have been other cases where animals have been bred for different behavioral traits to help further domestication. One of those cases was focused on German shepherds and the heritability of the following seven different behavioral traits: self-confidence, nerve stability, temperament, hardness, sharpness, defense drive, and fighting drive[29]. Nerve stability, hardness, and sharpness were already defined in Section II of this paper. Ruefenacht et al. defined self-confidence as the ability to react to new situation in a "calm, interested, self-confident, fearless, uninhibited, dauntless, attentive, and friendly" manner without showing any signs of aggression or distrust[29]. Temperament was defined as the physical flexibility and intensity of the dog's reaction to different situations. Defensive drive referred to the ability and desire of the dog to guard and protect the handler if threatened. Fighting drive is similar to defensive drive, but it refers to the ability and desire of self-confident dogs to attack an attacker, or the enemy. All of the dogs in this experiment took a standardized behavior test from the Swiss German Shepherd breeding club, and all of the results from this test have been stored in a database since 1978. This experiment looked at the correlations between the heritability estimates of different behavioral traits, and all of the correlations among traits were positive, and displayed a moderate to high relationship. These results suggest that all of these traits could have a common genetic background. The results also indicate that their selective breeding process seems to be more effective for some traits than others. For example, the mean breeding values for nerve stability and reaction to gunfire increased relatively quickly after around 1990, while some of the other traits, such as defense drive and hardness, seem to have decreased consistently since the start of this experiment[29]. This case indicates that there are more behavioral traits than the ones Guiding Eyes for the Blind focuses on that can be selected for through breeding.

Another case where animals are bred based on behavioral traits to further domestication efforts is an experiment that focuses on captive foxes[10]. This experiment did not use heritability estimates, but it did selectively breed foxes for over 45 years to possess more social behaviors that can be associated with domestication. Foxes were bred to be able to approach humans fearlessly and non-aggressively. They tested the effectiveness of their breeding process by examining the foxes' responses to different tests, such as finding hidden food, and how the foxes responded to non-verbal cues from a human trying to help them complete the task. The results indicate that the experimental foxes responded positively to human cues[10]. Therefore, the use of selective breeding for behavioral traits can further the domestication of foxes and helps to make the foxes more sociable.

There was also a case that selectively bred Wistar rats for high or low anxiety-related behavior for several generations[19]. The experimenters did not use heritability, but they made the rats go through a type of maze, for every generation, and whichever rats had the most and least pronounced anxiety scores were mated to produce the next generation. These mated rats were divided into two lines: high anxiety-related behavior (HAB) and low anxiety-related behavior (LAB). In addition to the mazes, these rats were put into open fields and went through a forced swim test. The LAB rats were more active and exploratory in the open fields, and they struggled more during the forced swim test than the HAB rats, which shows that the breeding process used was effective in producing different behavioral traits in these rats[19]. These results indicate that by selectively breeding for different anxiety levels, the activity of rats is also affected. This shows that it is possible to breed for behavioral traits in rats.

Another instance of breeding for behavioral traits is examined in a case that focused on breeding against damaging behaviors, such as feather pecking, in laying hens[5]. This study addressed the problem of identifying specific birds that were pecking or being pecked, especially in large groups of birds. Selective breeding has already been shown to be successful in producing animals that are less likely to perform this type of damaging behavior. However, this study proposed and examined the possibility of combining sensor technology used to monitor animals and genomic methods to identify the feather peckers and victims. The sensor technologies examined were ultra-wideband, radio frequency identification, and computer vision. The genomic methods examined included methods to identify biomarkers and genes to improve the behavioral traits in poultry, such as studying the genomes and gene expression in these hens. This study concluded that by combining these two methods for selection, the occurrences of these damaging behaviors in poultry could decrease over time[5]. This study further demonstrates that multiple species can be bred for behavioral traits.

Overall, these cases demonstrate that heritability estimates and/or breeding for behavioral traits can be applied to more than just dogs and to more than just one type of behavioral trait. However, it would be beneficial if more breeders started to look at breeding for behavioral traits and applying heritability estimates to their methods of selectively breeding. As of right now, heritability estimates are used for many cases of breeding, but a lot of these cases do not use heritability estimates to breed for behavior. However, using these estimates to breed for behavioral traits would be a beneficial supplementation to the breeding process.

Conclusion

The hypothesis of this thesis was supported by the current research, because GEB uses heritability estimates to breed for desirable behavioral traits, such as personality, harness sensitivity, and noise fear, and has been successful in improving these traits overtime (GEB, 2019, unpublished data; unreferenced). Guiding Eyes for the Blind may be one of the major programs that use heritability estimates in their selective breeding process, but other breeders are also implementing them in their breeding process in order to increase the chances of the offspring inheriting desirable behavioral traits. Additionally, multiple genes and genomic regions were found to be associated with behavioral traits both in dogs and in foxes, and some of these regions and associated chromosomes were even found to be related to each other between the two species. On top of that, within the dog species, some chromosomes and genomic regions were found to be associated with the same or related behaviors between different dog breeds.

Also, people have bred some other species for desirable behavioral traits. For example, rats and foxes were experimentally bred to determine if certain behavioral traits could be inherited, which the results showed that they could. These cases also demonstrated that by successfully breeding for specific behavioral traits, further domestication could be achieved. Overall, this thesis demonstrated that behavioral traits can be selected for during breeding, and there are a few ways to do so, one of which being using heritability estimates.

In terms of what conclusions from this thesis mean on a larger scale, the related chromosomes and genomic regions between different species could imply that there are specific chromosomes or genomic regions in all animals that are associated with the behavioral traits of animals. This could be used to further domesticate animals, as well as to begin domesticating wild animals. Also, many people are concerned with the behaviors of animals and how those behaviors affect humans, so knowing that there are ways to selectively breed for specific behavioral traits could help ease the worry of those people. However, there is a potential problem with breeding for behavioral traits. When a particular trait is selected for, that selection could cause changes in other traits that were not selected, which is called a correlated response. This correlated response could be positive and result in both the selected and unselected traits undergoing a positive change, but it could also be negative. A negative correlated response would result in an improvement in the selected trait, but a negative/worsening change in the unselected trait (GEB Breeding Manual, 2019, unpublished data; unreferenced). This correlated response could be due to co-selected traits (traits that are selected and inherited together) or linked genes (genes that are inherited together and are located on the same chromosome)[1]. For example, if breeders select an easy-to-handle trait, that could result in the dogs being too sensitive to touch (GEB Breeding Manual, 2019, unpublished data; unreferenced). So, despite the possibility of furthering domestication using heritability and breeding for behavioral traits, it is important to keep the potential consequences in mind.

Regarding what other research could be done about this topic, there is a lot of further research that could be done. While there are multiple cases where breeders are using heritability estimates to increase the chances of the offspring inheriting desirable behavioral traits, this method does not appear to be widespread among breeders yet. More research should be done regarding what other behavioral traits have a strong genetic association, especially for other species besides dogs. There should also be further research done on determining if there are any specific chromosomes or genes, within or between species, that are associated with behavioral traits. The amount of further research that could be done is essentially limitless, because there are so many aspects to breeding for behavioral traits and using heritability estimates. However, it would be ideal if more research was done about this topic and that information became more widespread, because breeding for behavioral traits and using heritability estimates could become the next big step in domestication.

Appendix

Table 2. Genetic regions that have been associated with behavioral traits.

Chromosome(s)	Gene(s)	Locus (Loci)	Associated Trait(s)
VVU12			Tame behavior (foxes) Active versus passive behaviors (foxes)[18]
	GTG21 GTF21RD1		Hypersociability (dogs)[33]
	Oxytocin receptor gene	rs8679684 (SNP) 19131AG (SNP)	Friendliness toward strangers (dogs)[16]
	Oxytocin receptor gene	-212AG (SNP)	Proximity seeking toward a human (dogs)[16]
Canine chromosome 26	SEZ6L	BICF2G630798942 (SNP)	Duration of close proximity to humans and duration of seeking physical contact with humans (dogs)[27]
Canine chromosome 26	ARVCF	BICF2S23712115 (SNP) BICF2S23712114 (SNP)	Duration of seeking human physical contact (dogs)[27]
Chromosome 18		BICF2P964118 (SNP)	Agitated when ignored (dogs)[13]
Chromosome 4		BICF2P696817 (SNP)	Barking tendency (dogs)[13]
Chromosome 1		BICF2G630792579 (SNP)	Fetching (dogs)[13]
Chromosome 4		BICF2P844921 (SNP) BICF2P456276 (SNP) BICF2P73495 (SNP) BICF2P519369 (SNP)	Fetching (dogs)[13]
Chromosome 22		BICF2S2314224 (SNP)	Fetching (dogs)[13]
Chromosome 20		BICF2P846231 (SNP)	Noise fear (dogs)[13]
Chromosome 9		BICF2G630832223 (SNP)	Non-owner-directed aggression (dogs)[13]
Chromosome 2		BICF2P612229 (SNP)	Unusual behavior (dogs)[13]

Table 3. Behavioral traits that are important to Guiding Eyes for the Blind, and their heritabilities (if applicable).

Trait	Heritability (h^2)
Temperament and overall trainability (Confidence, distraction, ease of handling) (GEB Breeding Manual, 2019, unpublished data; unreferenced)	
Personality (difference between shyness and boldness) (GEB Breeding Manual, 2019, unpublished data; unreferenced)	0.25[30]
Harness sensitivity (GEB Breeding Manual, 2019, unpublished data; unreferenced)	0.36 (GEB, 2019, unpublished data; unreferenced)
Noise Fear (GEB Breeding Manual, 2019, unpublished data; unreferenced)	0.26 (GEB, 2019, unpublished data; unreferenced)
Dog Distraction (GEB Breeding Manual, 2019, unpublished data; unreferenced)	0.06 (GEB, 2019, unpublished data; unreferenced)

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