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Genetic evaluation of traits in a standardized behavioral test for potential guide dog puppies using crossbreed models

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ABSTRACT

Two thousand one hundred twenty-seven potential guide dog puppies of 2 breeds and their crosses underwent a standardized applied-stimulus behavioral test at 6 weeks of age. The responses of the puppies were scored on a 7-point scale according to either responsiveness (reaction to human assessor) or confidence (reaction to environmental stimuli) on stimuli comprising: following when called, retrieve, gentle restraint, noise, stroking, a toy squirrel, encouragement to go through a tunnel, and encouragement to go over a ramp. It has been shown previously that some of these stimuli showed association with success in guide dog training. The results of each component of the test were analyzed using restricted maximum likelihood univariate animal models, and 8 of the 11 estimated heritabilities were significantly different from zero. Most of the crossbreeding parameter estimates were not detectably larger than zero, likely reflecting the small size of the dataset and the relatively close relationship between the 2 pure breeds. These results suggest that the behavioral test results (and the estimated breeding values produced from them) could be useful in identifying which puppies to use as breeding stock.

Introduction

The Guide Dogs for the Blind Association in the United Kingdom (hereafter referred to as Guide Dogs) is the largest breeder and trainer of working dogs in the world, and most of its guide dogs are bred by the organization (Guide Dogs for the Blind Association, 2013b). The 3 most numerous breeds and crosses used are Labrador retriever cross golden retriever, Labrador retriever, and golden retriever. In 2011, coinciding with the 80th anniversary of guide dog partnerships in the UK, a purpose-built National Breeding Centre opened allowing an increase in the number of puppies bred annually to 1,500 (Guide Dogs for the Blind Association, 2013a). Traditionally, Guide Dogs and other guide dog breeding organizations internationally have relied on phenotypic data when making selection decisions, mainly on health and behavioral traits. Behavior, like health, is complex, that is determined by both genetic and environmental factors (MacKenzie et al., 1986).

Guide Dogs place prospective guide dog puppies with volunteer puppy walkers at approximately 7 weeks of age, and the puppies remain with them until they are around 14 months old. Throughout this period, they undergo regular behavioral assessments. Dogs which pass all behavioral and health assessments either enter training at approximately 14 months old or become a brood bitch or stud dog. Training lasts 34 weeks on average, and dogs continue to undergo behavioral assessments throughout this period before commencing work as guide dogs at about 1½ to 2 years old. Selection of individuals for training or breeding could be achieved much earlier if behavioral test results of young stock were demonstrated to be predictive of success as a guide dog, and more accurate selection could be achieved if such results were shown to be heritable and selection criteria focused on estimated genetic liability.

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The heritability (h^2) of a trait expresses the proportion of the total phenotypic variance that is attributable to additive genetic variation (and so ranges from 0 to 1), indicating the reliability of the phenotypic value of an individual as a guide to its breeding (genetic) value (Falconer & Mackay, 1996). Phenotypic variation in traits which are barely heritable (h^2 approaching zero) is largely comprised of nonadditive genetic variance and environmental variance, for example, through nutrition or climate. Traits with a heritability >0.4 are considered highly heritable (Bourdon, 2000) and phenotypes are a useful guide to breeding value. The heritability of a trait reflects, and may be estimated from, the degree of resemblance between relatives. The animal model enables estimation of the heritability of a trait by assessing the phenotypic covariance between all pairs of relatives in a population (Lynch & Walsh, 1998). This approach is particularly useful for extracting the maximum information from multigenerational but sometimes patchy pedigrees (Kruuk & Hadfield, 2007).

The basic premise of quantitative genetics is that, if the relationships between individuals in a population are known, useful inferences about the inheritance of traits for which phenotypic data are available can be made without explicit knowledge of the genetic loci involved (Wilson et al., 2010). The ideal data set on which to use quantitative genetic techniques is one comprising data on a large number of individuals in a well-connected pedigree (Wilson et al, 2010). Quantitative genetic analysis of complex traits can yield best linear unbiased predictor estimated breeding values (EBVs) in addition to heritability estimates. The EBV of an individual for a particular trait can be calculated using phenotypic data from itself and all relatives, with the data being weighted according to the relevant genetic relationship (Nicholas, 2010). EBVs are a more accurate metric for selection than phenotypes of individuals alone (when $h^2 < 1$): they provide a more reliable indicator of the genetic liability of a trait than the phenotype itself, which is crucial since only genes are inherited across generations.

An American guide dog organization, The Seeing Eye Inc. has made use of EBVs for the selection of breeding stock since early 1995 (Leighton, 1997). At The Seeing Eye, EBVs are calculated for (1) hip score, (2) distraction index, (3) a temperament score reflecting trainability as a guide dog, and (4) body weight. These EBVs are then combined to produce an overall index which is the primary basis for making selection decisions (Leighton, 1997).

The golden retriever crossed with the Labrador retriever (GR × L) has been the most successful of all the breeds and crosses Guide Dogs have tried, combining the gentleness of the golden retriever with the willingness of the Labrador retriever (Freeman, 1991). Scott et al (1976) predicted that first-generation (F1) crosses between Labrador retrievers and golden retrievers should achieve higher average success than either parent breed and that there was a good probability that the performance level would be raised even higher with an associated reduction in training time and expense. These predictions appear to have been correct. In a study of German shepherd dogs, Labrador retrievers, golden retrievers, and GR × L born between 1999 and 2004 at The Seeing Eye, the GR × L had the highest probability of qualifying as a guide dog at 59% (Ennik et al., 2006). It was postulated that this could be due both to the benefits of breed differences and heterosis.

When 2 inbred lines are crossed, F1 hybrids typically show an increase in the mean phenotypic value in the traits that previously suffered a reduction due to inbreeding or, more simply, the performance lost due to inbreeding is generally restored by crossing (Falconer & Mackay, 1996). Often this improvement in performance exceeds the midparent breed mean and even the better of the 2 parental breed means too—this is the phenomenon of heterosis or hybrid vigor. Although heterosis is frequently observed in F1 crosses, much of its effect is lost in the subsequent F2 generation, and in some cases, this decline in trait performance is greater than would be seen if it were only due to the loss of heterosis. If the F2 progeny have substantially lower performance than the average of the original parental breeds this is due to the phenomenon of recombination loss, in which breed-specific epistatic effects on any given trait are broken during recombination of the gametes of the F1 generation (Lynch and Walsh, 1998).

As Guide Dogs use a large number of F1 crosses (and a smaller number of backcrosses to one of the parental breeds) between Labrador retrievers and golden retrievers, and of both pure breeds, crossbreed models are appropriate for the genetic analysis of behavioral data. Guide Dogs' dataset, which includes a large pedigree containing purebred and crossbred dogs, also enables the quantification of genetic parameters such as heterosis and recombination loss relating to behavior in dogs for the first time.

Various models of puppy testing have been trialled by working dog organizations internationally in attempts to improve selection for their respective programs (e.g., Scott & Bielfelt, 1976; Goddard & Beilharz, 1986; Wilsson & Sundgren, 1998; Slabbert & Odendaal, 1999; Russenberger, 2012). It has been suggested that testing puppies at 6 to 8 weeks of age may be advantageous, as puppies are motivated to approach unknown people during this period in contrast to greater wariness before and after this age (Serpell & Jagoe, 1995).

Guide Dogs has developed a puppy test named the Puppy Profiling Assessment (PPA) to assess the behavior of puppies before placement with puppy walkers at approximately 7 weeks of age, using a series of controlled stimuli. It was developed to be feasible, standardized and its criterion validity has been assessed, under the Taylor and Mills (2006) framework for the development of behavioral tests for dogs. Asher et al. (2013) analyzed the results of a pilot study of the PPA involving 587 puppies and showed that 5 of the 11 PPA stimuli were associated with later success in guide dog training. The PPA was refined based on the findings of Asher et al. (2013) and is now used routinely by Guide Dogs with all puppies at approximately 6 weeks of age before they are placed with puppy walkers. The aim of the present study was to investigate genetic and known environmental factors, and the crossbreeding parameters of heterosis, recombination loss and breed fraction, relating to the PPA to determine whether there was potential for developing EBVs for any PPA components. This would allow better informed decisions to be made about which dogs to use as breeding stock. More accurate selection of breeding stock would hopefully increase the proportion of dogs bred by Guide Dogs which successfully qualify as guide dogs.

Methods

Data description

Between 2012 and 2014, 2,592 puppies were assessed using the PPA protocol. Only Labrador retrievers, golden retrievers, and crosses between these 2 breeds were included in subsequent analyses, and only those individuals which had been bred by Guide Dogs, resulting in the exclusion of 465 puppies. The final dataset analyzed therefore included 2,127 puppies. These puppies were included in Guide Dogs' pedigree file, which contained 53,283 dogs. This was used for convenience rather than preparing a new pedigree file just containing the puppies' direct ancestors; many of the individuals in the pedigree file will not have been related to the puppies which underwent the PPA, but their inclusion will not have had any impact on the precision of variance component estimates.

A MATLAB (The MathWorks, Inc., Natick, Mass, USA) program was created to assign litter identification numbers to puppies with dates of birth and parental identification numbers in