Investigation of breeding strategies to increase the probability that German shepherd dog and Labrador retriever dog guides would attain optimum size

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ABSTRACT: An optimum-sized dog guide weighs 18 to 32 kg and measures 53 to 64 cm in height at the withers when mature body size is attained. Effects of selection index with and without restrictions, independent trait selection, directional selection, stabilizing selection, and negative assortative mating were modeled using data from German shepherd dogs and Labrador retrievers raised by the Seeing Eye, Inc., Morristown, NJ from 1979 to 1997. The selection goals were to decrease mature weight and mature height in German shepherd dogs and to decrease mature weight and increase mature height in Labrador retrievers. Mature weights were recorded for 1,333 German shepherd dog offspring and their 69 dams and 17 sires, and 1,081 Labrador retriever offspring and their 51 dams and 13 sires. Mature heights also were recorded for offspring and parents, including 871 German shepherd dogs from 70 dams and 15 sires, and 793 Labrador retrievers from 40 dams and 13 sires. Selecting on mature weight alone produced the highest aggregate genetic-economic gain for German shepherd dogs compared with the selection indices with and without restrictions, generating a 2.10-kg decrease in mature weight and a correlated 0.36-cm decrease in mature height. In Labrador retrievers, selecting for mature height alone produced the highest aggregate genetic-economic gain but caused an increase in mature weight. Weighting the two traits equally but in the opposite direction without restrictions was the only index that produced the desired effect of decreasing mature weight and increasing mature height in Labrador retrievers. Response to selection for one generation of directional selection for a single trait included a 0.50-kg decrease in mature weight for German shepherd dogs, a 0.59-kg decrease in mature weight for Labrador retrievers, a 0.18-cm decrease in mature height for German shepherd dogs, and a 0.91-cm increase in mature height for Labrador retrievers.

Increasing the percentage of dogs attaining optimum size may decrease the cost of production for the Seeing Eye, Inc., because fewer dogs would need to be raised and trained to provide assistance to the same number of blind individuals.

Key Words: Body Weight, Dogs, Height, Selection


Introduction

Dog guides facilitate independence and confidence by allowing their owners to travel safely without assistance from other people. The Seeing Eye, Inc., Morristown, NJ, pioneered dog guide training in the United States in 1929. Seventy years later, 9,000 U.S. dog guide teams were active (Eames et al., 2001). Dog guides accompany their owners everywhere and must physically fit into spaces not designed to accommodate dogs.

Extreme physical dimensions can be a limiting factor in determining whether a dog becomes a guide. Dog guides need to have sufficient weight in order to guide their owners safely, but heavier dogs may be too large and difficult for owners to handle. A dog guide must also be the appropriate height for the owner’s reach. A dog guide of optimal size weighs 18 to 32 kg and measures 53 to 64 cm at the withers when mature size is attained. A selection protocol to increase the proportion of dogs within the desirable range for mature weight and height would decrease the cost of production because fewer dogs could be raised to benefit the same number of individuals.

Previous research (Helmink et al., 2001) determined that Seeing Eye German shepherd dogs and Labrador retrievers outside the optimum range for mature weight tended to be too heavy. Among dogs outside of the optimum range for mature height, German shepherd dogs...
tended to be too tall, whereas Labrador retrievers tended to be too short. Positive genetic correlations between mature weight and mature height were found for both breeds (Helmink et al., 2001).

The objective of this research was to investigate the probable outcomes of different breeding strategies on the Seeing Eye population of German shepherd dogs and Labrador retrievers, including selection indices, independent trait selection, directional selection, stabilizing selection, and negative assortative mating.

Materials and Methods

Data

Data were recorded for German shepherd dogs and Labrador retrievers raised by the Seeing Eye, Inc., from 1979 to 1997, including 25,494 weight observations on 4,427 dogs and a single height observation on 2,420 dogs. Dams were mated to an average of 3.2 (SD = 1.7) sires and produced an average of 4.1 (SD = 2.6) litters. Although no environmental corrections were made to the data, the dogs were housed at the Seeing Eye from birth to 6 to 8 wk of age and later from 12 to 14 mo of age until placed with a blind person or retained for breeding. Puppy-raising personnel who provided the dogs with individualized socialization and basic training during time away from the facility were given standardized care procedures.

Mature Weight

Mature weight was defined as the last weight recorded from 300 to 600 d of age because weight fluctuations were common when puppy-raising personnel returned the dogs to the facility at around 12 to 14 mo of age. The weights were not adjusted for age or environmental effects. Offspring from dam and sire pairs with available mature weights had mature weights recorded for 1,333 German shepherd dogs from 271 litters by 69 dams and 1,081 Labrador retrievers from 210 litters by 51 dams and 13 sires. The number of littermates included for German shepherd dogs was 1 to 10 dogs with an average of 4.7 (SD = 2.3) dogs per litter. One to 11 dogs per litter were represented for Labrador retrievers and averaged 4.7 (SD = 2.3) dogs per litter.

Categorizing dams and sires based on mature height followed the same procedure as mature weight except both dams and sires were divided into five groups (Shortest, Short, Average, Tall, and Tallest). The groups were less equalized for mature height than mature weight because mature height groups often included just one height rather than a range of heights. Nine sires were in the Tallest group, three sires were in the Average group, two sires were in the Tall group, and one sire was in the Short group for German shepherd dogs. For Labrador retrievers, there were six sires in the Average group, four sires in the Short group, two sires in the Tall group, and one sire in the Tallest group. No height data were available on mates of the Shortest sires; therefore, no progeny were included in the study. Mean mature height and mean age when mature height was recorded were calculated for dams and sires by breed. The mean mature height of the progeny included just one height rather than a range of heights. Nine sires were in the Tallest group, three sires were in the Average group, two sires were in the Tall group, and one sire was in the Short group for German shepherd dogs. For Labrador retrievers, there were six sires in the Average group, four sires in the Short group, two sires in the Tall group, and one sire in the Tallest group. No height data were available on mates of the Shortest sires; therefore, no progeny were included in the study. Mean mature height and mean age when mature height was recorded were calculated for dams and sires by breed. The mean mature height of the progeny included in each mating type and the number of progeny above, below, and within the optimum range of 53 to 64 cm was also determined.

Selection of Replacement Breeders

At the time of this research, selection of replacement breeders occurred within the first month of training upon return to the facility. Decisions about which dogs to consider as candidates for breeding were first based on the overall selection index value, which was a function of three estimated breeding values: hip score, distraction index, and trainability score. Distraction index is a measure of hip joint laxity (Smith et al., 1990, 1993).
Medical soundness was an additional consideration. It was assumed that no purposeful selection on weight or height had been done previously.

**Breeding Strategies**

Index selection and independent trait selection were applied using available data to predict the outcome of concurrent and individual selection, respectively, on mature weight and mature height. Additional breeding strategies, including directional selection, stabilizing selection, and negative assortative mating were applied retrospectively to each trait for one generation to move toward the selection goals using available data. A chi-squared test was used to test changes in the number of progeny within the acceptable range for mature weight and mature height in the retrospective analyses. The response to selection and correlated response to selection were also calculated for directional selection to predict the resulting outcomes. For German shepherd dogs, selection for both traits was in the decreasing direction. For Labrador retrievers, the goal of selection was to decrease mature weight and increase mature height.

**Selection Index.** Index selection uses all the information available about each individual’s breeding value and the relationship between the traits involved (Falconer and Mackay, 1996). Selection index was developed for application to animal breeding by Hazel (1943). Genetic and phenotypic (co)variance components determined by Helmink (2000) and different economic weights for mature weight and mature height were incorporated into several selection indices with and without restrictions using the procedure of Hogsett and Nordskog (1958).

Several economic weights were used to calculate index weights ($b_i$) for mature weight and mature height, respectively: 1:1, 2:1, 1:2, 3:1, and 1:3 because previously used economic weights were not found in the literature. The selected ratios allowed for a general survey of results that could be used to further delineate the most appropriate economic weights in future applications. Index weights were used to calculate genetic change ($\Delta i$) in each trait associated with one standard deviation of selection in the index. In order to compare the aggregate genetic-economic gain ($\Delta H$) among indices with different economic relationships, economic weights were calculated using a constant standard deviation of the aggregate genotype ($\sigma_H$) determined from the 1:1 relationship for each breed. Restricted selection indices were also calculated in which the genetic change in one trait was held to zero.

**Independent Trait Selection.** The effect of selecting on each trait alone was also determined using the selection index method by weighting the trait of interest at 1 and weighting the other trait at 0.

**Directional Selection.** In directional selection, individuals are selected for breeding to move the population mean toward the desired extreme. Both breeds tended to be too heavy rather than too light. Therefore, progeny were evaluated of all mating types except those involving the Heaviest dams and sires. In cases where progeny data of the Heaviest dams and/or sires were not available, the additional effect of excluding the Heavy dams or sires was also considered. The effect of directional selection on mature height was determined using the same method with the objective of moving the population toward the lower extreme in German shepherd dogs and toward the upper extreme in Labrador retrievers.

In addition to determining the retrospective effects of directional selection, the predicted response was calculated to quantify the changes in mature weight and mature height. The response to selection ($R$) for each scenario was determined by $R = h^2 \times (x_s - x)$, where $h^2$ is heritability of the trait, $x_s$ is the trait mean for the selected parents, and $x$ is the trait mean for the population from which the parents were selected. Heritabilities used in the calculations were 0.57 and 0.44 for mature weight in German shepherd dogs and Labrador retrievers, respectively, and 0.35 and 0.46 for mature height in German shepherd dogs and Labrador retrievers, respectively (Helmink et al., 2001). Population averages from Helmink (2000) were also used in the calculations: 28.37 kg and 29.53 kg for mature weight in German shepherd dogs and Labrador retrievers, respectively, and 60.89 cm and 56.71 cm for mature height in German shepherd dogs and Labrador retrievers, respectively. Both the parental and population means covered all the years of data to create the largest possible sample size.

The correlated response to selection was also calculated to determine the effect of directional selection for mature weight on mature height and vice versa. Genetic parameters determined by Helmink et al. (2001) were used in the calculations, including the genetic correlation between mature weight and mature height of 0.3 for German shepherd dogs and 0.7 for Labrador retrievers.

**Stabilizing Selection.** Stabilizing selection occurs when individuals not included in either extreme of a trait are selected for breeding and results in the population moving closer to the mean value of that trait. Matings that included neither the Lightest nor Heaviest dams and/or sires were evaluated for mature weight within breed. The same general procedure was used to evaluate the effect of stabilizing selection on mature height.

**Negative Assortative Mating.** Negative assortative mating does not involve the selection of which animals to breed, but rather the way in which the animals are mated. The effect of negative assortative mating was retrospectively examined by evaluating the progeny of mating types at opposite extremes or close to the mean. The mating types included for mature weight in both breeds were as follows: Lightest dams with Heaviest sires, Light dams with Heavy sires, Average-light dams and Average-heavy dams with Average sires, Heavy
Table 1. Mean mature weight, mature height, and ages when mature weight and mature height were recorded for dams and sires of German shepherd dogs and Labrador retrievers

<table>
<thead>
<tr>
<th>Parents</th>
<th>Mature weight, kg</th>
<th>Age, d</th>
<th>Mature height, cm</th>
<th>Age, d</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SEM</td>
<td>Mean</td>
<td>SEM</td>
</tr>
<tr>
<td>Dams</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>GS</td>
<td>25.8</td>
<td>0.3</td>
<td>457</td>
<td>8</td>
</tr>
<tr>
<td>LR</td>
<td>25.8</td>
<td>0.4</td>
<td>464</td>
<td>9</td>
</tr>
<tr>
<td>Sires</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>GS</td>
<td>28.1</td>
<td>0.6</td>
<td>471</td>
<td>17</td>
</tr>
<tr>
<td>LR</td>
<td>28.8</td>
<td>0.7</td>
<td>493</td>
<td>17</td>
</tr>
</tbody>
</table>

*German shepherd dog.
Labrador retriever.

dams with Light sires, and Heaviest dams with Lightest sires. For mature height, the mating types included the following: Shortest dams with Tallest sires, Short dams with Tall sires, Average dams with Average sires, Tall dams with Short sires, and Tallest dams with Shortest sires.

Results and Discussion

Parental and Progeny Trends

Table 1 gives the mean mature weight, mean mature height, and mean age when each was recorded for dams and sires by breed. Mean mature weights for dams and sires were similar between breeds. Dams and sires of German shepherd dogs were taller than dams and sires of Labrador retrievers. In general, progeny of lighter or shorter dams and sires had lower mature weights or mature heights than progeny of heavier or taller dams and sires (data not shown). A comparison of basic statistics for the mean of each progeny group indicated normality (Helmink, 2000).

In terms of the optimum range of 18 to 32 kg for mature weight, only 6 of 1,333 German shepherd dog progeny were below the optimum range, whereas 163 dogs (12%) were above the optimum range (Table 2). Further scrutiny found that mature height was recorded for 117 of the 163 dogs above the optimum range for mature weight. One of the 117 dogs had a mature height of 53 cm (the minimum mature height in the optimum range) and 90 of the 117 dogs (77%) had a mature height of at least 64 cm (the maximum value in the optimum range). Thus, German shepherd dogs that were too tall also tended to be too heavy.

In contrast to German shepherd dogs, Labrador retrievers had more progeny that were too short than were too tall. Only 9 out of 793 progeny were above the optimum range, whereas 82 dogs (10%) were below the optimum range for mature height. Mature weights were available for 36 of the 82 dogs that were too short. Only 1 of the 36 dogs had a weight outside the optimum range; however, the dog was too heavy rather than too light. Five of the nine dogs that were too tall had mature weights available. Two of the five dogs had a mature weight greater than 32 kg. Based on the available data, Labrador retrievers were more likely than German shepherd dogs to be within the optimum range for mature weight even if their mature height was outside the acceptable range, and vice versa.

When evaluating these results, it is important to note that the measurements were taken between 300 and 600 d of age and no further adjustments for age and environmental effects were made. The limited availability of corresponding mature weight or mature height data for the progeny may also have an effect on the interpretation of related trends in mature weight and height.

Breeding Strategies

Selection Index and Independent Trait Selection. Tables 4 and 5 list the index weights ($b_i$), genetic change for each trait ($\Delta i$) associated with one standard devia-
Table 2. Number of German shepherd dog progeny with mature weights below, within, and above the optimum range of 18 to 32 kg

<table>
<thead>
<tr>
<th>Sire weight group</th>
<th>Lightest</th>
<th>Light</th>
<th>Average</th>
<th>Heavy</th>
<th>Heaviest</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lightest</td>
<td>D</td>
<td>D</td>
<td>D</td>
<td>X</td>
<td>N</td>
</tr>
<tr>
<td>Below</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>In range</td>
<td>20</td>
<td>15</td>
<td>18</td>
<td>29</td>
<td>3</td>
</tr>
<tr>
<td>Above</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Light</td>
<td>D</td>
<td>D, S</td>
<td>D, S</td>
<td>S, N</td>
<td>X</td>
</tr>
<tr>
<td>Below</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>In range</td>
<td>63</td>
<td>42</td>
<td>39</td>
<td>62</td>
<td>12</td>
</tr>
<tr>
<td>Above</td>
<td>4</td>
<td>1</td>
<td>3</td>
<td>13</td>
<td>7</td>
</tr>
<tr>
<td>Average-Light</td>
<td>D</td>
<td>D, S</td>
<td>D, S, N</td>
<td>S</td>
<td>X</td>
</tr>
<tr>
<td>Below</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>In range</td>
<td>41</td>
<td>8</td>
<td>81</td>
<td>76</td>
<td>12</td>
</tr>
<tr>
<td>Above</td>
<td>0</td>
<td>0</td>
<td>17</td>
<td>12</td>
<td>3</td>
</tr>
<tr>
<td>Average-heavy</td>
<td>D</td>
<td>D, S</td>
<td>D, S, N</td>
<td>S</td>
<td>X</td>
</tr>
<tr>
<td>Below</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>In range</td>
<td>82</td>
<td>24</td>
<td>78</td>
<td>114</td>
<td>3</td>
</tr>
<tr>
<td>Above</td>
<td>9</td>
<td>10</td>
<td>10</td>
<td>20</td>
<td>4</td>
</tr>
<tr>
<td>Heavy</td>
<td>D</td>
<td>D, S, N</td>
<td>D, S</td>
<td>S</td>
<td>X</td>
</tr>
<tr>
<td>Below</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>In range</td>
<td>64</td>
<td>21</td>
<td>64</td>
<td>55</td>
<td>0</td>
</tr>
<tr>
<td>Above</td>
<td>5</td>
<td>3</td>
<td>11</td>
<td>8</td>
<td>0</td>
</tr>
<tr>
<td>Heaviest</td>
<td>N</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Below</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>In range</td>
<td>39</td>
<td>31</td>
<td>24</td>
<td>43</td>
<td>0</td>
</tr>
<tr>
<td>Above</td>
<td>4</td>
<td>2</td>
<td>7</td>
<td>8</td>
<td>0</td>
</tr>
</tbody>
</table>

a Mating types and retrospective results are also indicated for directional selection (D), stabilizing selection (S), and negative assortative mating (N). Some mating types (X) were excluded from all breeding strategies.

b Lightest = 23.6 to 25.4 kg, Light = 26.3 to 27.2 kg, Average = 27.7 to 29.0 kg, Heavy = 29.5 to 30.4 kg, Heaviest = 30.8 to 36.3 kg.

c Lightest = 17.7 to 22.7 kg, Light = 23.1 to 24.5 kg, Average-light = 24.7 to 25.9 kg, Average-heavy = 26.3 to 27.2 kg, Heavy = 27.7 to 28.6 kg, Heaviest = 29.0 to 34.0 kg.

The results for Labrador retrievers were not as substantial because a positive genetic correlation between the two traits contravened the goal of decreasing mature weight and increasing mature height. Further research is needed to understand the relative economic values of mature weight and mature height in German shepherd dogs so an optimal level of change can be achieved in both traits.
Investigation of breeding strategies in dogs

<table>
<thead>
<tr>
<th>Table 3. Number of Labrador retriever progeny with mature weights below, within, and above the optimum range of 18 to 32 kg&lt;sup&gt;a&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Sire weight group</strong>&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td><strong>Dam weight group</strong>&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
<tr>
<td><strong>Below</strong></td>
</tr>
<tr>
<td><strong>In range</strong></td>
</tr>
<tr>
<td><strong>Above</strong></td>
</tr>
<tr>
<td><strong>Below</strong></td>
</tr>
<tr>
<td><strong>In range</strong></td>
</tr>
<tr>
<td><strong>Above</strong></td>
</tr>
</tbody>
</table>

<sup>a</sup>Mating types and retrospective results are also indicated for directional selection (D), stabilizing selection (S), and negative assortative mating (N). Some mating types (X) were excluded from all breeding strategies.

<sup>b</sup>Lightest = 23.6 to 25.4 kg, Light = 26.3 to 27.2 kg, Average = 27.7 to 29.0 kg, Heavy = 29.5 to 30.4 kg, Heaviest = 30.8 to 36.3 kg.

<sup>c</sup>Lightest = 17.7 to 22.7 kg, Light = 23.1 to 24.5 kg, Average-light = 24.7 to 25.9 kg, Average-heavy = 26.3 to 27.2 kg, Heavy = 27.7 to 28.6 kg, Heaviest = 29.0 to 34.0 kg.

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<table>
<thead>
<tr>
<th>Table 4. Results of the selection indices and independent trait selection for mature weight and mature height in German shepherd dogs&lt;sup&gt;a&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Economic weights (weight, height)</strong>&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>(--1.00, --1.00)</td>
</tr>
<tr>
<td>(--1.00, --1.00)</td>
</tr>
<tr>
<td>(--1.00, --1.00)</td>
</tr>
<tr>
<td>(--1.18, --0.59)</td>
</tr>
<tr>
<td>(--1.18, --0.59)</td>
</tr>
<tr>
<td>(--1.18, --0.59)</td>
</tr>
<tr>
<td>(--0.73, --1.46)</td>
</tr>
<tr>
<td>(--0.73, --1.46)</td>
</tr>
<tr>
<td>(--0.73, --1.46)</td>
</tr>
<tr>
<td>(--1.12, --0.41)</td>
</tr>
<tr>
<td>(--1.24, --0.41)</td>
</tr>
<tr>
<td>(--1.24, --0.41)</td>
</tr>
<tr>
<td>(--0.56, --1.68)</td>
</tr>
<tr>
<td>(--0.56, --1.68)</td>
</tr>
<tr>
<td>(--0.56, --1.68)</td>
</tr>
<tr>
<td>(--1.35, 0)</td>
</tr>
<tr>
<td>(0, --2.15)</td>
</tr>
</tbody>
</table>

<sup>a</sup>i: index weights, Δ: genetic change associated with one standard deviation of selection in the index, ΔH: aggregate genetic-economic gain, σ<sub>H</sub>: standard deviation of the aggregate genotype, τ<sub>H</sub>: accuracy of the index.

<sup>b</sup>Rounded to two decimal places, adjusted to equate σ<sub>H</sub> between indices.
lecting for height alone. It is likely that the optimum economic values to fulfill the selection goals for Labrador retrievers are between the ratios of -1:1 and -1:2 for mature height and mature weight, respectively. A closer analysis of economic values between these two ratios is needed.

**Directional Selection.** Excluding the Heaviest dams and the Heaviest and Heavy sires for mature weight in German shepherd dogs decreased ($P = 0.04$) the number of progeny outside the optimum range from 169 to 76, whereas the number of total progeny decreased from 1,333 to 736 (Table 2). This corresponded to a decrease in the percentage of progeny outside the optimum range for mature weight from 13% (169/1,333) to 10% (76/736). Although the decrease in the percentage of individuals outside the optimum range was significant, it was lower than expected because mating types other than the upper extremes produced progeny outside the optimum range.

In Labrador retrievers, removing the Heaviest and Heavy dams and the Heaviest sires (Table 3) decreased ($P = 0.08$) the percentage of progeny outside the optimum range for mature weight from 18% (192/1,081) to 15% (98/643). Retrospectively, directional selection increased the probability of that dogs would attain mature weight within the optimum range for both breeds, but the increase was small and not significant for Labrador retrievers.

The outcomes for mature height (data not reported) were more difficult to predict because much of the data came from mating types targeted for removal in directional selection. For German shepherd dogs, the majority of progeny (76%) came from the Tallest sires, whereas almost half the Labrador retriever progeny (49%) came from shorter dams and/or sires. It may be necessary to determine whether the number of progeny per mating type was indicative of the entire breeding program before directional selection is considered for mature height.

Table 6 and 7 give the response to selection and correlated response for each scenario described for directional selection in German shepherd dogs and Labrador retrievers. The mean mature weight (Table 6) and mature height (Table 7) of the parents was less than the mean of the population in both breeds. Results from excluding none of the parents provided a basis for comparing subsequent selection schemes. For German shepherd dogs, removing three of the heavier parental groups produced a 0.50-kg decrease in mature weight with a correlated decrease in mature height of 0.10 cm (Table 6). Removing the Tallest sires produced a 0.18 cm-decrease in mature height with a correlated decrease in mature weight of 0.10 kg (Table 7).

In Labrador retrievers, excluding three of the heavier parental groups produced a 0.59-kg decrease in mature weight and a correlated decrease of 0.34 cm in mature height (Table 6). Removing the Shortest dams and sires produced a 0.91-cm increase in mature height with a correlated increase in mature weight of 0.73 kg (Table 7). Directional selection successfully moved the traits in each breed in favorable directions; however, due to the positive genetic correlation between the traits, the correlated response was in an unfavorable direction for Labrador retrievers.

**Stabilizing Selection.** Excluding mating types at both extremes increased ($P = 0.17$) the percentage of progeny outside the optimum range for mature weight from 13% (169/1,333) to 14% (112/777) for German shepherd dogs.

### Table 5. Results of the selection indices and independent trait selection for mature weight and mature height in Labrador retrievers

<table>
<thead>
<tr>
<th>Economic weights (weight, height)</th>
<th>Restrictions</th>
<th>b$_{WT}$</th>
<th>b$_{HT}$</th>
<th>$\Delta$Weight, kg</th>
<th>$\Delta$Height, cm</th>
<th>$\Delta$H</th>
<th>$\sigma_H$</th>
<th>$\tau_H$</th>
<th>Relative efficiency, %</th>
</tr>
</thead>
<tbody>
<tr>
<td>(-1.00, 1.00)</td>
<td>None</td>
<td>-0.2719</td>
<td>0.2342</td>
<td>-0.88</td>
<td>0.06</td>
<td>0.95</td>
<td>1.8</td>
<td>0.51</td>
<td>73</td>
</tr>
<tr>
<td>(-1.00, 1.00)</td>
<td>$\Delta WT = 0$</td>
<td>-0.1633</td>
<td>0.2839</td>
<td>-</td>
<td>-0.81</td>
<td>0.81</td>
<td>1.8</td>
<td>0.44</td>
<td>62</td>
</tr>
<tr>
<td>(-1.00, 1.00)</td>
<td>$\Delta HT = 0$</td>
<td>-0.2749</td>
<td>0.2228</td>
<td>-0.94</td>
<td>-</td>
<td>0.94</td>
<td>1.8</td>
<td>0.51</td>
<td>73</td>
</tr>
<tr>
<td>(-0.96, 0.48)</td>
<td>None</td>
<td>-0.3130</td>
<td>0.0294</td>
<td>-1.60</td>
<td>-0.86</td>
<td>1.13</td>
<td>1.8</td>
<td>0.61</td>
<td>87</td>
</tr>
<tr>
<td>(-0.96, 0.48)</td>
<td>$\Delta WT = 0$</td>
<td>-0.0787</td>
<td>0.1368</td>
<td>-</td>
<td>0.81</td>
<td>0.39</td>
<td>1.8</td>
<td>0.21</td>
<td>30</td>
</tr>
<tr>
<td>(-0.96, 0.48)</td>
<td>$\Delta HT = 0$</td>
<td>-0.2649</td>
<td>0.2147</td>
<td>-0.94</td>
<td>-</td>
<td>0.91</td>
<td>1.8</td>
<td>0.49</td>
<td>70</td>
</tr>
<tr>
<td>(-0.60, 1.21)</td>
<td>None</td>
<td>-0.1002</td>
<td>0.3868</td>
<td>0.70</td>
<td>1.23</td>
<td>1.07</td>
<td>1.8</td>
<td>0.58</td>
<td>83</td>
</tr>
<tr>
<td>(-0.60, 1.21)</td>
<td>$\Delta WT = 0$</td>
<td>-0.1970</td>
<td>0.3425</td>
<td>-</td>
<td>0.81</td>
<td>0.98</td>
<td>1.8</td>
<td>0.53</td>
<td>75</td>
</tr>
<tr>
<td>(-0.60, 1.21)</td>
<td>$\Delta HT = 0$</td>
<td>-0.1658</td>
<td>0.1344</td>
<td>-0.94</td>
<td>-</td>
<td>0.57</td>
<td>1.8</td>
<td>0.31</td>
<td>44</td>
</tr>
<tr>
<td>(-0.90, 0.30)</td>
<td>None</td>
<td>-0.3071</td>
<td>-0.0335</td>
<td>-1.67</td>
<td>-1.02</td>
<td>1.19</td>
<td>1.8</td>
<td>0.65</td>
<td>92</td>
</tr>
<tr>
<td>(-0.90, 0.30)</td>
<td>$\Delta WT = 0$</td>
<td>-0.0488</td>
<td>0.0849</td>
<td>-</td>
<td>0.81</td>
<td>0.24</td>
<td>1.8</td>
<td>0.13</td>
<td>19</td>
</tr>
<tr>
<td>(-0.90, 0.30)</td>
<td>$\Delta HT = 0$</td>
<td>-0.2465</td>
<td>0.1998</td>
<td>-0.94</td>
<td>-</td>
<td>0.85</td>
<td>1.8</td>
<td>0.46</td>
<td>65</td>
</tr>
<tr>
<td>(-0.38, 1.13)</td>
<td>None</td>
<td>-0.0227</td>
<td>0.3953</td>
<td>1.06</td>
<td>1.39</td>
<td>1.17</td>
<td>1.8</td>
<td>0.63</td>
<td>90</td>
</tr>
<tr>
<td>(-0.38, 1.13)</td>
<td>$\Delta WT = 0$</td>
<td>-0.1847</td>
<td>0.3211</td>
<td>-</td>
<td>0.81</td>
<td>0.91</td>
<td>1.8</td>
<td>0.50</td>
<td>71</td>
</tr>
<tr>
<td>(-0.38, 1.13)</td>
<td>$\Delta HT = 0$</td>
<td>-0.1036</td>
<td>0.0840</td>
<td>-0.94</td>
<td>-</td>
<td>0.36</td>
<td>1.8</td>
<td>0.19</td>
<td>27</td>
</tr>
<tr>
<td>(-0.75, 0)</td>
<td>Selecting on mature weight alone</td>
<td>-1.70</td>
<td>-1.21</td>
<td>1.27</td>
<td>1.8</td>
<td>0.69</td>
<td>98</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(0, 0.89)</td>
<td>Selecting on mature height alone</td>
<td>1.42</td>
<td>1.46</td>
<td>1.29</td>
<td>1.8</td>
<td>0.70</td>
<td>100</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Index weights, $\Delta$: genetic change associated with one standard deviation of selection in the index, $\Delta H$: aggregate genetic-economic gain, $\sigma_H$: standard deviation of the aggregate genotype, $\tau_H$: accuracy of the index.*

*Rounded to two decimal places, adjusted to equate $\sigma_H$ between indices.*
Table 6. Response to selection in mature weight and correlated response in mature height for different scenarios of directional selection to decrease mature weight in German shepherd dogs and Labrador retrievers

<table>
<thead>
<tr>
<th>Parent group(s) excluded</th>
<th>German shepherd dogs</th>
<th>Labrador retrievers</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Parental mean</td>
<td>Response to selection,</td>
</tr>
<tr>
<td></td>
<td>mature weight, kg</td>
<td>mature weight, kg</td>
</tr>
<tr>
<td>None</td>
<td>26.19</td>
<td>−1.24</td>
</tr>
<tr>
<td>Heaviest dams, heaviest sires</td>
<td>25.50</td>
<td>−1.64</td>
</tr>
<tr>
<td>Heaviest dams, heaviest sires, heavy sires</td>
<td>25.31</td>
<td>−1.74</td>
</tr>
</tbody>
</table>

(Table 2) and remained at 18% (87/490) for Labrador retrievers (Table 3). Based on the available data, stabilizing selection did not significantly change the percentage of individuals within the optimum range for mature weight.

Results for mature height (data not shown) were similar to the results determined for directional selection, likely because the data available were concentrated in the mating types already excluded in directional selection.

Because both populations were much closer to one extreme or the other for mature weight and mature height, stabilizing selection may not be the optimal solution. For example, decreasing the number of lighter individuals as well as the number of heavier individuals would keep the average mature weight about the same.

For this data set, the average mature weight was 28.37 ± 0.10 kg and 29.53 ± 0.10 kg for German shepherd dogs and Labrador retrievers, respectively (Helmink, 2000). Both values are higher than the center of the optimum (25 kg) and should be moved toward the intermediate value to maximize the number of individuals within the acceptable range.

Negative Assortative Mating. The retrospective application of negative assortative mating for mature weight in German shepherd dogs (Table 2) resulted in an increase (\( P = 0.7 \)) of progeny outside the optimum range from 13% (169/1,333) to 15% (49/334). Progeny outside the optimum range were just as likely, or, in some cases, more likely, to occur from matings of opposite extremes or individuals near the mean mature weight.

A similar result was found for mature weight in Labrador retrievers (Table 3). The percentage of progeny outside the optimum range for mature weight resulting from negative assortative mating was 20% (39/197), an increase (\( P = 0.9 \)) from the percentage of progeny outside the optimum range based on all mating types (192/1,081 = 18%). Based on the available data, negative assortative mating did not increase the probability of either breed attaining optimum mature weight; numerically, the percentage of progeny within the acceptable range was decreased.

The effect of negative assortative mating on mature height (data not reported) was difficult to assess because no data were available for progeny of the Shortest dams and Tallest sires or the Tallest dams and Shortest sires for both breeds. Based on available data, the percentage of individuals outside the optimum range for German shepherd dogs decreased (\( P = 0.04 \)) from 17% (147/871) to 0 (0/40). Although negative assortative mating seemed to be successful in increasing the probability that German shepherd dogs would attain mature height within the optimum range, the lack of data for some of the mating types was certainly a factor.

In Labrador retrievers, the percentage of progeny outside the optimum range for mature height resulting

Table 7. Response to selection in mature height and correlated response in mature weight for different scenarios of directional selection to decrease mature height in German shepherd dogs and increase mature height Labrador retrievers

<table>
<thead>
<tr>
<th>Parent group(s) excluded</th>
<th>German shepherd dogs</th>
<th>Labrador retrievers</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Parental mean</td>
<td>Response to selection</td>
</tr>
<tr>
<td></td>
<td>mature height, cm</td>
<td>mature height, cm</td>
</tr>
<tr>
<td>None</td>
<td>59.78</td>
<td>−0.39</td>
</tr>
<tr>
<td>Tallest sires</td>
<td>59.26</td>
<td>−0.57</td>
</tr>
</tbody>
</table>

None

Shortest dams

Shortest dams, shortest sires

57.57 0.40 0.32
from negative assortative mating decreased \((P = 0.4)\) from 11\% (91/793) to 8\% (20/237). However, the results do not reflect any extreme mating between opposites due to lack of data. As is similar to mature weight, negative assortative mating did not appear to be the best solution for increasing the probability that either breed would attain mature size within the optimum range.

When evaluating the results from all of these breeding strategies, it is important to note that only one generation of response was evaluated. Although the study provides an example for practical application to other canine populations, direct utilization of the results on other populations is not recommended because the data were derived from a single population. Further research to confirm the genetic parameters and determine accurate economic weights for mature weight and mature height would increase the certainty of these results.

### Implications

Several breeding strategies were investigated to increase the probability that Seeing Eye dogs would attain optimal size. Directional selection was more successful than stabilizing selection or negative assortative mating at increasing the percentage of dogs within the acceptable range for mature weight because both breeds were closer to one extreme. Results for mature height were difficult to interpret due to limited data. Use of a selection index for mature weight and mature height may be the best way to concurrently select for both traits because the correlation between the two traits would be considered. Further investigation is necessary to determine the most appropriate economic weights for mature weight and mature height. Additional research to adjust weight and height measurements for environmental effects and confirm genetic parameter estimations would increase the confidence in these findings, which provide some of the first published results on selection of growth traits in dogs.

### Literature Cited


