

POPULATION STRUCTURE  
AND GENETICS OF LONGEVITY IN A COLONY OF  
DOG GUIDES

A Dissertation

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John B. Cole  
B. S., Louisiana State University, Baton Rouge, 1994  
M. S., Louisiana State University, Baton Rouge, 1996  
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## **DEDICATION**

This work is dedicated to the author's family and friends, in particular his wife, Misty. Without their love, encouragement, support, and sacrifice this work would not have been possible.

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## ABSTRACT

The objectives of this study were the description of changes in genetic diversity in a colony of dog guides since its founding, and the investigation of the genetics of longevity in that population. Two breeds of dog, German Shepherds (GS) and Labrador Retrievers (LR), were evaluated.

There were rapid increases in average pairwise relationship in both breeds, although the average was approximately one-third higher in the GS population than in the LR population. A similar trend was observed for average inbreeding. In the current generation, relationship and inbreeding for all animals averaged 25.3% and 26.2% in GS and 15.5% and 22.0% in LR, respectively. Effective founder numbers initially decreased in GS until generation 3, and then increased steadily. There was a constant increase in effective founder number in LR after founding. A similar pattern was seen for effective ancestor number as well. Founder genome equivalents were initially higher in the GS but decreased over time in both breeds. New breeding stock should be imported in order to reduce the levels of inbreeding and relationship in this colony.

Data on longevity for 1,403 GS and 1,816 LR dogs who worked as guides were used to estimate genetic parameters for working life. Two measures of working life were considered: working life to 18 months post-graduation (EWL) and working life beyond 18 months post-graduation (LWL). Survival analysis was used to estimate the sire component of variance and estimated breeding values (EBVs). Linearized heritability estimates were small: 0.032 and 0.045 for EWL and 0.016 and 0.032 for LWL in GS and LR, respectively. Genetic trend

was estimated by regression of EBVs on year. No trend was observed for either trait in either breed, suggesting that historical selection criteria were not effective in improving working life. An antagonistic relationship may exist between aptitude for guide work and risk of culling for temperament.

# CHAPTER 1

## INTRODUCTION

Dog guide producers are subject to economic constraints which are different than those of commercial livestock or companion animal producers. The organizations which produce dog guides are not able to recover the cost of breeding, raising, training, and placing animals from the dog owner. When guide dogs must be replaced, producers incur additional costs, and owners often experience great emotional and psychological distress when a partner must be replaced. As a result, it is important that dog guides have long working lives.

In order to develop a breeding program to improve the working life of dog guides, variance components and breeding values must be estimated. Methods for the estimation of breeding values require *a priori* estimates of (co)variance components. The heritability of working life, as well as its correlation with other traits of interest, determines the speed with which the population mean value for working life may be changed. Estimated breeding values are used for ranking individuals with respect to genetic merit for a trait, as well as for predicting the genetic merit of offspring.

Estimates of the heritability of productive life in dairy cattle, the species which has been most intensively studied, and other livestock species are low to moderate. The magnitude of the heritability of longevity is likely to be low in dog guides, as well. If positive correlations exist between longevity and other traits of interest, a selection index which includes correlated traits and longevity can be constructed to identify genetically superior individuals.

The value of longevity has been noted and studied in many livestock species, especially in dairy cattle. Replacement costs are high for both dairy heifers and trained dog guides, motivating breeders to select for longer lifespans. However, unlike dairy cattle, dog guides do not generate revenue during their lifespan, emphasizing the cost of a suboptimal breeding program. Dog guides may indirectly generate revenue by improving their handler's productivity, as well as by reducing the cost to society of caring for their handler. Clearly it is desirable to maximize longevity, and more particularly the productive life (PL), of dog guides. Selection for improved longevity may have been underway in the dog guide population for many years, as dogs in service do not have to compete economically with potential replacements.

Longevity is a measure of total lifespan (i.e. days or months from birth to death), while productive life is the amount of time an individual is able to successfully perform the task for which they were bred. Two different measures of productive life (PL) will be studied in order to determine which is most useful for making decisions in a dog guide population. Early Working Life is the amount of time, in days, a dog works during their first 540 days post-graduation, while Late Working Life is the amount of time a dog spends working from 541 days post-graduation until they are retired.

The extent to which PL may be improved through a breeding program depends largely on the amount of genetic variability that exists for PL in the target population. Research in dairy cattle has shown that the proportion of variability in PL that is under genetic control is approximately 5 to 12% (Vollema

and Groen, 1998.). While this low level seems disappointing, it is important to note that PL is strongly correlated with other traits of importance in dairy cattle. If the results are similar in guide dogs, PL may be improved through the use of a selection index that combines information on several important traits into a single numerical quantity. In addition to determining the proportion of variability for PL under genetic control, several related quantities, termed (co)variance components, must be estimated as well.

Once (co)variance component estimates have been obtained, a model for the estimation of breeding values can be developed. The model can account for genetic and environmental effects shown to have a significant effect on the traits under study. The work of Helmink et al. (2001) with growth data in guide dogs may be used to help identify such effects. The resulting breeding values may be used for the accurate selection of individuals of high genetic merit for use as parents of successive generations. Even a small number of genetically superior individuals can have a strong influence on the genetic merit of a population. In the United States, two sires account for 25% of the genes in the Holstein-Friesian breed of dairy cattle (Young and Seykora, 1996).

The early development of a selection program based on breeding values derived from performance data allows for the rapid realization of gains from selection. Gains from selection are cumulative, allowing breeders to improve genetic merit for even moderately heritable traits. Further, as data accumulate over the life of a breeding program, selection becomes increasingly more accurate.

It is important to understand the precise structure of a population when evaluating long-term breeding objectives. Tools such as coefficients of inbreeding and relationship are useful, but they do not capture all of the relevant information about changes in population structure and genetic diversity. Conservation geneticists have developed several tools for describing the structure of populations, and these will be combined with genetic parameters to characterize the current dog guide population. Changes in those parameters can be used to monitor the health of the population and inform management decisions.

The development of a sound scientific breeding program is important for the long-term health and success of a population. It is particularly important to understand the genetics of traits such as longevity and productive life in a population of working animals. Such research based on a dog guide population has never been reported in the scientific literature. Given the high cost of replacing a working guide dog, there is a compelling need for such information.

The objectives of this study are the description of the genetic structure of an existing dog guide population and the characterization of genetic components of longevity and productive life in that population to determine their suitability for use as selection criteria. The Seeing Eye, Inc. of Morristown, NJ, is the oldest and largest trainer of dog guides in the United States and has provided the data necessary for this study. This population has been described in Leighton (1997).

## **CHAPTER 2**

### **REVIEW OF LITERATURE**

#### **Measures of Genetic Variation**

Coefficients of inbreeding and relationship (Wright, 1922) have been commonly used to describe the genetic diversity in livestock populations (Young and Seykora, 1996). Inbreeding coefficients represent an individual's expected genetic homozygosity due to the relatedness of its parents. Coefficients of relationship describe the expected proportion of genes two individuals share due to their relatedness. These are relative measures that depend on such factors as the completeness and depth of pedigrees. Over time, these coefficients change in response to breeding and culling decisions, and they may be used as indicators of the genetic variability of a population. Rapid methods for calculating coefficients of inbreeding and relationship for large populations have been implemented (Wiggans, VanRaden, and Zuurbier, 1995).

Populations under study rarely conform to the theory established for the use of coefficients of inbreeding (Wright, 1931). Lacy (1989) and Boichard et al. (1997) proposed measures of genetic variation based on ideas from conservation genetics. Lacy (1989) proposed the idea of the number of founder equivalents in assessing populations. A founder is an ancestor whose parents are unknown. If all founders contribute to the population equally, then the founder equivalent is equal to the number of founders. When founders contribute unequally to the population, the number of founder equivalents decreases. Boichard et al. (1997) developed the idea of founder ancestor equivalents, which

is the minimum number of ancestors necessary to explain the genetic diversity of the current population. Founder ancestor equivalents account for bottlenecks, unlike founder equivalents, and are more accurate in populations undergoing intense selection. Caballero and Toro (2000) discussed the relationships among these and other measures of diversity in small populations, and demonstrate their use (Toro et al., 2000).

Roughsedge et al. (1999) used average coefficients of inbreeding, average coefficients of relationship, founder equivalent numbers, and founder ancestor numbers to document the decrease in genetic diversity in the British dairy cattle population over the last 25 years. Changes in founder equivalent number and founder ancestor number reflected the use of a small number of influential individuals to improve the genetic merit of that population. Accompanying changes in average inbreeding and relationship did not accurately reflect that loss of diversity. Such results highlight the need for additional tools when assessing complex populations.

### **Genetics of Longevity**

Measures of longevity have been of interest to livestock breeders due to their relationship to farm profitability. In the case of the dog guide, longevity is of interest due to the high cost of producing a trained animal and the stress to the owner of replacing a guide. Longevity is typically defined as productive life, which is the amount of time an animal spends producing milk or fiber (VanRaden and Klaaskate, 1993). Productive life has been studied in dairy cattle and poultry (Ducrocq et al., 2000). VanRaden and Wiggans (1995) implemented genetic

evaluations for PL of dairy cattle in the United States using a linear model. Their model accounted for many factors known to affect productive life, including herd, year of birth, and genetic merit of herdmates (VanRaden and Wiggans, 1991). Ducrocq et al. (1988b) reported a log scale heritability of PL of 0.09. VanRaden and Klaaskate reported the heritability of PL as 0.09 using a linear model (1993). Jairath et al. (1998) reported the heritability of functional herd life, the ability of a cow to withstand involuntary culling, as 0.03. Vollema and Groen (1998) also reported heritabilities of 0.06 from both linear and survival models from a study of Dutch dairy cattle. Boettcher et al. (1999) reported heritability estimates of 0.04, 0.07 and 0.09 for linear, threshold and survival models, respectively. Dürr et al. (1999) reported heritabilities of 0.19 and 0.15 for true and functional herd life in Canadian dairy cattle. Ducrocq et al. (2000) estimated heritabilities for two measures of longevity in laying hens as 0.48 and 0.19 on a log scale. Beaudreau et al. (1995) demonstrated that a number of factors, including disease, can increase a cow's risk of being culled, reducing her productive life.

### **Models for Survival Data**

Several different models for analyzing survival data have been proposed (Cox, 1972; Cox and Oakes, 1984; Le, 1997). Survival models are based on probability distributions which model the process of survival and death over time. One of the key features which distinguish survival data from other data is the presence of incomplete records. Complete records, defined as lifetime records ending in the death or retirement of an animal, are termed uncensored. Incomplete records, defined as records that do not end in death or

retirement at the end of the study period, are termed censored. A key difference between linear model methods and survival analysis is that survival analysis allows the evaluation of censored and uncensored records simultaneously. The length of censored records provides a lower bound for estimating longevity, but if such records are deleted or adjusted inappropriately, biased estimates of breeding values will result (Ducrocq, 1994). Factors affecting survivability in a time-dependent manner may also be accounted for using survival analysis.

Famula (1981) used an exponential model to analyze data including censored records. Wolynetz and Binns (1983) expanded on this work with models using Weibull or lognormal distributions. Their results showed that those distributions are more suitable for use with dairy cattle data than the exponential. Using techniques based on the work of Cox (1972), Smith and Quaas (1984) used nonparametric proportional hazards models to estimate genetic parameters. Proportional hazards models are models under which the hazard function may be partitioned into a baseline hazard function, which is independent of risk factors, and a scaling factor which is independent of time. While such models allow more freedom when specifying the model, they are very computationally demanding, precluding their use with large datasets. Cox-type models based on the Weibull distribution greatly simplify computations and may be used for large datasets (Ducrocq et al., 1988a).

The Weibull distribution is relatively simple, and is very flexible. (Evans et al., 2000). It is commonly used in reliability and survival analysis to

model failure-time data. The two-parameter Weibull distribution has a probability density function of:

$$f(x; \lambda, \rho) = \frac{\rho x^{\rho-1}}{\lambda^\rho} e^{-(x/\lambda)^\rho}$$

a cumulative density function of:

$$F(x; \lambda, \rho) = 1 - e^{-(x/\lambda)^\rho}$$

and a mean and variance of:

$$E(x; \lambda, \rho) = \lambda \Gamma\left[\frac{(\rho+1)}{\rho}\right]$$

and

$$E(x^2; \lambda, \rho) = \lambda^2 \Gamma\left[\frac{(\rho+2)}{\rho}\right] - \Gamma\left[\frac{(\rho+1)}{\rho}\right]^2$$

The Weibull distribution is very flexible, and can model increasing, decreasing, or constant hazards. Maximum likelihood estimates of the shape and scale parameters,  $\lambda$  and  $\beta$ , may be easily obtained.

Kachman (1999) provides an excellent overview of modern methods for survival analysis. Suppose that animal  $i$  is alive and survives until failure (death) at some time,  $T_i$ . Such failure may be modeled as a random process which depends on fixed effects,  $\boldsymbol{\beta}$ , such as sex and random effects,  $\mathbf{u}$ , such as additive genetic merit. These risk factors may be combined into a vector of factors,  $\boldsymbol{\eta}_i = \mathbf{x}_i\boldsymbol{\beta} + \mathbf{z}_i\mathbf{u}$ . The probability that animal  $i$  survives to time  $t$ , given the risk function  $\boldsymbol{\eta}_i$ , is called the survival function:

$$S(t; \eta_i) = Pr(T_i \geq t) = 1 - F(t; \eta_i) \\ = \int_t^{\infty} f(t; \eta_i) dt$$

where  $F(t; \eta_i)$  is the cumulative density function of  $T_i$  and  $f(t; \eta_i)$  is the probability density function of  $T_i$ . Hazard functions, which measure the risk of failure of individual  $i$  at time  $t$ , are used to model survival functions. The hazard function,  $\lambda(t; \eta_i)$ , is related to the survival function as:

$$\lambda = \frac{f(t; \eta_i)}{S(t; \eta_i)}$$

The survival function may be obtained from the hazard function as:

$$S(t; \eta_i) = e^{-\Lambda(t; \eta_i)}$$

where:

$$\Lambda(t; \eta_i) = \int_0^t \lambda(t; \eta_i) dt$$

The cumulative and probability density functions follow as:

$$F(t; \eta_i) = 1 - S(t; \eta_i) \\ f(t; \eta_i) = \lambda(t; \eta_i) S(t; \eta_i)$$

The hazard function must be nonnegative, positive at time  $t$ , and may increase or decrease over time.

Weibull models are able to model both increasing and decreasing hazards, and are commonly used in survival analysis (Ducrocq et al., 1988a,b).

The hazard and survival functions for a Weibull distribution may be written as:

$$\lambda(t; \eta_i) = \rho \lambda (\lambda t)^{\rho-1} \\ S(t; \eta_i) = e^{-(\lambda t)^\rho}$$

The rate parameter,  $\rho$ , determines the shape of the hazard function. When  $\rho < 1$  the hazard is increasing,  $\rho = 1$  the Weibull model reduces to the simpler exponential model, and  $\rho > 1$  the hazard is decreasing. In most cases, it is expected that  $\rho > 1$ , which corresponds to an increasing risk of failure as time increases. Weibull distributions may be used to fit proportional hazards models (Smith and Quaas, 1984; Smith and Allaire, 1986).

A proportional hazards model is a model in which the hazard function for animal  $i$  is the product of a time-dependent term, which does not depend on risk factors, and a risk-dependent term, which does not depend on time. Under such a model the the hazards of two individuals are assumed to be proportional to the difference of their risks. The survival and hazard functions may be rewritten as:

$$\begin{aligned} S(t; \eta_i) &= e^{-t^\rho e^{\rho \ln(\lambda)}} \\ &= e^{-\Lambda(t; 0) e^{\eta_i}} \end{aligned}$$

and

$$\begin{aligned} \lambda(t; \eta_i) &= \rho t^{(\rho-1)} e^{\rho \ln(\lambda)} \\ &= \lambda_0(t) e^{\eta_i} \end{aligned}$$

where the hazard function is the product of two terms,  $\lambda_0(t)$  and  $e^\eta$ , which correspond to the basic shape of the hazard function and the risk relative to the baseline hazard, respectively.

The vector of risks,  $\boldsymbol{\eta}$ , can be a combination of fixed and random effects, such as  $\boldsymbol{\eta} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{u}$ . Under Weibull survival models, equations similar to the mixed model equations of Henderson (1984) may be written and solved to

obtain solutions for the fixed and random effects. Iterative methods for solving the appropriate estimating equations are available (Ducrocq et al., 1988a; Kachman, 1999).

Heritability estimates may be obtained from sire model estimates of additive genetic variance (Ducrocq and Casella, 1996). Given an estimate of sire genetic variance,  $\sigma_s^2$ , and a log-gamma herd-year-season effect,  $\gamma_h$ , the heritability of longevity on a log scale is:

$$h_{\log}^2 = \frac{4\sigma_s^2}{\sigma_s^2 + \Psi^{(1)}(\gamma_h) + \frac{\pi^2}{6}}$$

where  $\Psi^{(1)}(\gamma_h)$  is the trigamma function evaluated at  $\gamma_h$ . Heritability is expressed on a log scale because a Weibull proportional hazards model represents a particular class of log-linear model. Log scale heritabilities should be interpreted carefully as they represent the heritability of the trait when no records are censored. An approximation of heritability on a linear scale may be approximated using a Taylor series expansion of  $h_{\log}^2$  around its mean (Ducrocq and Casella, 1996):

$$h^2 = \frac{4\sigma_s^2}{e\left(\frac{1}{\rho}\right)^{2\nu} \times \left(\sigma_s^2 + \Psi^{(1)}(\gamma_h) + \frac{\pi^2}{6}\right)} = \frac{h_{\log}^2}{e\left(\frac{1}{\rho}\right)^{2\nu}}$$

where  $\nu = \Psi(\gamma_h) - \log_e(\gamma_h) - \text{Euler's constant}$  and  $\Psi(\gamma_h)$  is the digamma function evaluated at  $\gamma_{h_{ncv}}$ . Dürr et al. (1999) reported that linear-scale heritabilities computed using this method were much higher than estimates obtained using traditional linear model approaches.

Weibull models are theoretically satisfying, but are computationally demanding. Meuwissen et al. (2002) analyzed simulated data using proportional hazards, linear, and binary models. Correlations between estimated breeding values and true breeding values were similar for all three methods. Vollema and Groen (1998) reported that variance components estimates were similar for survival and linear models. Dürr et al. (1999) also reported comparable results from their work with Canadian Holsteins. Linear models provide estimates of breeding values and variance components that are similar to those obtained from survival models. However, given the tractable size of the data sets in this study, survival models were used.

### **Quantitative Genetics in the Dog**

Relatively little research on quantitative genetics in dogs has been reported in the literature. Most of the published research deals with hip and elbow dysplasia, which are degenerative diseases of the skeleton (Kapatkin et al., 2002; Lust, 1997). Heritability estimates for hip dysplasia have ranged from 0.10 to 0.93 (Dist et al., 1991; Hedhammar et al., 1979; Leighton et al., 1977; Leighton, 1997; Leppänen et al., 2000; Lingaas and Klemetsdal, 1990; Mäki et al., 2000; Mäki et al., 2002a; Ohlerth et al., 2001; Reed et al., 2000; Swenson et al., 1997a,b; Wood et al., 2000a,b; Wood et al., 2002). Elbow dysplasia is a degenerative disease of the elbow, and is similar to hip dysplasia (Hayes et al., 1979). Estimates of the heritability of elbow dysplasia range from 0.10 to 0.77 (Grondalen and Lingaas, 1991; Guthrie and Pidduck, 1990; Mäki et al., 2000;

Mäki et al., 2002a; Studdert et al., 1991; Swenson et al., 1997b). To date, elbow dysplasia has not been observed to be a significant problem in dog guides.

Of greatest interest in this case are the studies by Guthrie and Pidduck (1990) on elbow dysplasia and Leighton (1997) on hip dysplasia. These studies present results from the breeding colonies of Guide Dogs for the Blind Association (UK) and The Seeing Eye, Inc. (US). Based on differential rates of occurrence of elbow dysplasia in each sex, Guthrie and Pidduck performed separate analyses for each sex, reporting heritabilities of 0.77 and 0.45 for males and females, respectively. It is not clear if the higher heritability in males versus females represents an actual difference or it is due to the relatively small sample size. Leighton (1997) reported heritabilities of 0.35 and 0.45 (no s.e. reported) for subjective hip score and distraction index, which are phenotypic measures of hip quality. These two measures are used in an index which has successfully reduced the likelihood of hip dysplasia by 21% for GS and 20% for LR, respectively.

Helmink et al. (2000) described breed and sex differences for growth curves in dog guides. They also estimated genetic parameters for growth traits in GS and LR using contemporary methodology (Helmink et al., 2001). Their model included fixed gender and birth year and random maternal and litter effects. Growth traits were found to be lowly- to moderately-heritable, with additive genetic effects explaining 14-53% and 26-46% of observed variation for those traits in GS and LR, respectively. It should be noted that conformation traits, such as height, have moderate to high heritabilities due to their relationship to skeletal

traits. Smith et al. (1998) showed that a 1 percent increase in inbreeding resulted in a loss of 6 days of productive life in Holstein cattle. It is reasonable to suppose that there might be a comparable effect in guide dogs. The literature suggests that data recorded on guide dogs is amenable to analysis using methods which have been developed and validated in other species.

Chase et al. (2002) reported heritabilities for principal components of skeletal traits of Portuguese Water Dogs. Thirty-four skeletal traits were measured from radiographs of 330 Portuguese Water Dogs. Four principal components (PC) accounted for 61% of phenotypic variation in the measured traits, and the PCs corresponded to overall skeletal size, pelvic structure-head and neck interactions, skull and limb length-skull width and height interactions, and skull and limb length-strength of limb and axial skeleton. Heritabilities ( $\pm$  s.e.) were  $0.23 \pm 0.06$ ,  $0.55 \pm 0.08$ ,  $0.24 \pm 0.06$ , and  $0.70 \pm 0.06$  for each of the first four PCs. The moderate-to-high heritabilities of these four PCs, as well as the interactions between the traits which load on each PC, provide an explanation for the speed with which canid phenotypes have diversified. These results also help provide an explanation for the success of breeding programs to reduce the incidence of canine hip dysplasia.

Hoffman et al. (2002) estimated variance components for eight traits measured during sheep dog trials in Germany. Two thousand seven hundred forty five records on 337 Border Collies were available. Heritabilities ranged from  $0.001 \pm 0.001$  to  $0.129 \pm 0.082$ . Repeatabilities of scores across events were low-to-moderate (0.1–0.5). These results are of interest because they provide an

estimate of the heritability of behavioral traits. Behavioral traits, in the form of an aptitude score, are used in a selection index by The Seeing Eye, Inc. These results should be interpreted carefully, however, due to the small number of individuals in the study.

Holmes (1998, 2000) has written enthusiastically about the potential of molecular genetics to improve animal health. Wilkie (1999) has also written extensively on this subject. While recent developments in canine molecular genetics are of great interest to the animal health community, they are unlikely to prove of great value to breeders of guide dogs at present. Most traits that pose problems to breeders, such as hip dysplasia and longevity, are under the control of a large number of genes. While some work has been done to dissect the architecture underlying complex traits in dogs (Chase et al, 2002), it is unclear how this information can be incorporated into a breeding program. As the cost of obtaining molecular marker data continues to decrease, and statistical tools for incorporating quantitative and marker data into animal model analyses improve, the potential utility of molecular genetics to the applied breeder increases. However, the results do not currently justify the costs of obtaining such data.

### **Dog Guide Teams**

While a relatively small proportion of the total blind populations in the United States and Great Britain use dog guides, dog guides are much more popular in Britain (Eames and Eames, 1989). This may be attributed to both structural differences in dog guide movements and cultural differences about pets between the two countries. Eames and Eames (1989) suggested that most

Americans do not know the function of a working dog guide. That lack of knowledge, combined with the emphasis on independence of mobility, may result in greater risks for American dog teams. In Britain there is much more reliance on public assistance in high-traffic situations, and assistive devices to improve the visibility of the team. It is conceivable that this could result in higher risks and shorter working lives for dog guides in the United States.

As of 1999, there were 8,999 active dog guide teams in the United States, and fifteen schools that trained 1,556 new teams that year. While there is a small number of teams in the U.S. relative to the population as a whole, the impact of dog guides on the lives of their owners is profound. Miner (2001) indicated that dog guide owners report increased independence, greater confidence, and improved socialization when using dog guides. It is also said that dog guide owners are better able to navigate complex landscapes, are able to travel farther more quickly than cane users, and are more useful to persons who are also deaf (Eames et al., 2001). Cane users who have developed a high degree of mobility are generally considered desirable candidates for dog guide ownership because they have good orientation and mobility skills (Milligan, 1999).

Owners and their dog develop very close attachments, and the retirement or death of a long-term guide can result in grief like that associated with the loss of a family member, although retirement is less distressing than death (Nicholson et al., 1995; Wellard, 1993). Sanders (2000) reported survey data which show that for many owners, their social identity is tightly bound with

with the dog. The acquisition of a guide is a transformative experience. Clearly it is desirable to maximize the working life of dog guides. Longer working lives result in decreased emotional trauma resulting from the end of human-dog partnerships and allow guide dog schools to provide animals to more people without the need to increase resources.

Koda and Shimoju (1999) reported gender-of-dog and gender-of-human effects when neutered dog guides and humans of various ages interacted. Female dogs approached sitting humans and initiated contact more readily than male dogs. When the human subjects were allowed to interact with the dogs, men initiated contact with dogs more often than women, and women more often than girls. These data may be useful for improving bonding in teams.

Dog guides encounter a wide variety of stimuli in their work, and excessive fearfulness of any of these stimuli may cause a dog to be unsuitable for use as a guide. Goddard and Beilharz (1982, 1983) showed that fearfulness could be decreased and suitability for use as a dog guide increased by a genetic selection program. Further work by the same authors indicated that it is best to evaluate potential dog guide behaviors which are directly relevant to that work (Goddard and Beilharz, 1984a). Activity in fearful situations is independent of activity in non-fearful situations, and dogs may increase or decrease activity when fearful. All measures of fearfulness were correlated, which suggests that efforts to reduce fearfulness in guide dogs should focus on stimulus situations directly relevant to that work (Goddard and Beilharz, 1984a). Decreasing

fearfulness may reduce auditory and visual exploration, allowing dogs to focus more intently on guide activities.

The Royal Guide Dogs Associations of Australia (Melbourne, Australia) (RGDAA) select dogs with desirable temperament based on a score assigned by a trainer after a series of five walks; the consistency of their evaluations were assessed by Murphy (1995). The Seeing Eye, Inc. and other dog guide schools use similar methods for assessing temperament. A reasonable degree of consistency was observed between trainers, but considerable time and money could be saved if trainers were able to refine their methods. Thirty percent of dogs given good assessment scores based on videotapes of walks were ultimately rejected as guides. Almost 70% of dogs with provisional ratings were rejected. Clearly this represents a considerable waste of dogs and resources.

Murphy (1998) reported results from a study designed to standardize descriptions of temperament used by the RGDAA as part of work to improve the accuracy of temperament assessment and reduce culling rates of dogs in training. Her results suggest that sets of behavioral characteristics should be used to evaluate dogs, rather than single behavioral elements. In contrast to this approach, Serpell and Hsu (2001) suggested that puppy raisers be used as sources of primary information about behavior. Their results showed a strong association between reasons for failure due to temperament and behavior described by puppy raisers. This suggests that the use of combined puppy raiser-trainer data could improve the accuracy of dog guide selection.

## **CHAPTER 3**

# **POPULATION GENETIC STRUCTURE OF A COLONY OF GERMAN SHEPHERD AND LABRADOR RETRIEVER DOG GUIDES**

### **Introduction**

The genetic structure of a population is of interest to animal breeders who are tasked with the management of a population. Information about the genetic structure of a population can be recovered from pedigrees when accurate records have been maintained. Pedigree information has been used for many years to assess the health of zoo and wild animal populations, but only recently have those methods been applied to larger domestic animal populations. Research on dairy cattle has shown that populations which use artificial insemination (AI) heavily generally possess less genetic variability. It is not clear if this is also the case in populations which do not make appreciable use of artificial insemination, but use intensely-selected sires and dams .

Average coefficients of inbreeding are commonly used to quantify the loss of genetic diversity in a population over time. However, inbreeding trend is only reliable as a measure of change in diversity when a population is closed to migration, randomly mating, and finite in size (Wright, 1931). Breeding colonies clearly violate these assumptions. Measures of genetic diversity commonly used in conservation genetics, such as effective founder number (Lacy, 1989) and effective ancestor number (Boichard et al., 1997), have recently been used to

analyze the rate of change in genetic diversity in several livestock species (Sölkner et al., 1998; Roughsedge et al., 1999; Toro et al., 2000).

Lacy (1989) proposed the use of effective founder number which uses information from the contributions of founders to the population under study. Those contributions are used to estimate the number of equally-contributing founders that would produce a population with the same diversity as the current population. Boichard et al. (1997) generalized the idea to consider the highest-contributing ancestors in the population rather than just the founders. The resulting measure, effective ancestor number, is the number of equally-contributing ancestors that would produce a population with the same diversity as the current population.

The objectives of this part of the study were 1) to estimate and evaluate measures of genetic diversity for German Shepherd (GS) and Labrador Retriever (LR) dog guides and 2) to propose management practices which will insure the long-term health and viability of this breeding colony.

Average coefficients of inbreeding and relationship, effective founder number, effective ancestor number, founder genome equivalents, and effective population size were estimated for each breed over a 25 year period. Generation intervals were estimated for each sex and breed using parental and litter birth dates. The ten most influential sires and dams in each breed were identified based on their average pairwise relationship to other dogs in the colony (Cockerham, 1967). Length of sire and dam service lives were also computed.

## Materials and Methods

Data were provided by the Seeing Eye, Inc., Morristown, NJ, and consisted of pedigrees of 4,699 GS and 3,573 LR dogs bred for use as guides. Not all dogs produced by The Seeing Eye are used as guides. Dogs were selected for use as parents at 24 months of age based on health, hip quality, and aptitude for guide work. Some animals used as parents subsequently worked as dog guides.

Founder animals were defined as individuals with unknown parents. In this data set, both parents were known or neither parent was known; there were no half-founders. The effective founder number was calculated as:

$$f_e = 1 / \sum(p_i^2)$$

where  $p_i$  is the proportion of genes contributed by ancestor  $i$  to the current population (Lacy, 1989). If all founders had contributed equally to the population, then  $f_e$  would be the same as the actual number of founders. When founders contribute to the population unequally,  $f_e$  is smaller than the actual number of founders. The greater the inequity in founder contributions, the smaller the effective founder number.

Lacy (1989) also defined the number of founder genome equivalents ( $f_g$ ) as a measure of genetic diversity. A founder genome equivalent is the number of founders which would produce a population with the same diversity of founder alleles as in the pedigree population assuming all founders contributed equally to each generation of descendants. Founder genome equivalents are calculated as:

$$f_g = 1 / \sum(p_i^2/r_i)$$

where  $p_i$  is the proportion of genes contributed by ancestor  $i$  to the current population and  $r_i$  is the proportion of founder  $i$ 's genes which are retained in the current population. Like  $f_e$ ,  $f_g$  accounts for unequal founder contributions. Unlike  $f_e$ ,  $f_g$  also accounts for the fractions of founder genomes lost from the pedigree through drift during bottlenecks. While  $f_g$  is the more accurate description of the amount of founder variation present in a population, it can only be calculated directly for simple pedigrees. For large or complex pedigrees, the number of founder genome equivalents must be approximated based on computer simulation of a large number of segregations through the pedigree.

In populations which have undergone a bottleneck, the effective number of founders computed using the previous equation is overestimated. Large contributions made by recent ancestors are more important to the population with respect to the loss of genetic diversity than equal contributions made long ago. Boichard et al. (1997) proposed a second measure of diversity to deal with such situations, the effective number of ancestors ( $f_a$ ), which considers the genetic contribution of all ancestors in the population, not just founders. The effective number of ancestors treats all ancestors in the population the same way.  $f_a$  is computed as :

$$f_a = 1 / \sum(q_i^2)$$

where  $q_i$  is the genetic contribution of the  $i^{\text{th}}$  ancestor not explained by the previous  $i-1$  ancestors. The ancestors with the greatest contributions are selected iteratively. The number of ancestors with a positive genetic contribution is less than or equal to the actual number of founders.

Coefficients of relationship and inbreeding were calculated using the method of Meuwissen and Luo (1992). Average and maximum coefficients of inbreeding were computed for the entire population and for all individuals with non-zero inbreeding for both breeds. The average relationship among all individuals in the colony born in a generation was computed for each breed. Theoretical and realized effective population sizes,  $N_{e(t)}$ , and  $N_{e(r)}$ , were estimated as (Falconer and MacKay, 1996):

$$N_{e(t)} = \frac{4 N_m N_f}{N_m + N_f}$$

and

$$N_{e(r)} = \frac{1}{2 \Delta f}$$

where  $N_m$  and  $N_f$  are the number of sires and dams in the population, respectively, and  $\Delta f$  is the change in population average inbreeding between generations  $t$  and  $t+1$ . Interpretation of  $N_{e(t)}$  can be problematic when  $\Delta f$  is calculated from incomplete or error-prone pedigrees. This is not believed to be a problem with the current data.

Founders were assigned generation codes of 0. All other animals were assigned generation codes as:

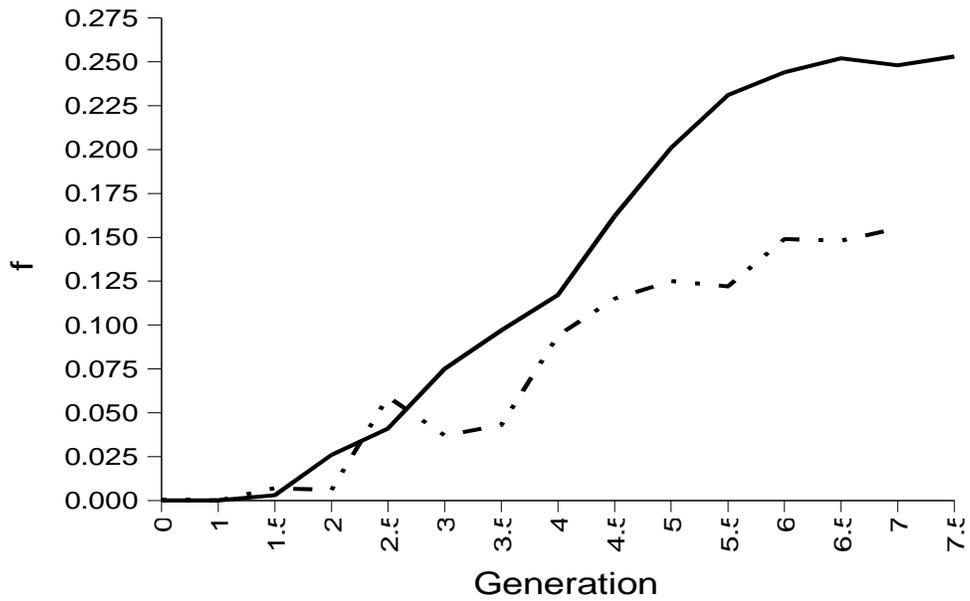
$$GC_o = \frac{(GC_s + GC_d)}{2} + 1$$

where  $GC_o$ ,  $GC_s$ , and  $GC_d$ , represent offspring, sire, and dam codes, respectively (Leighton, 1997). Larger generation codes indicate more opportunity for genetic selection because individuals with larger generation codes are the offspring of animals which have themselves been subjected to selection. In this study, generation coefficients were rounded to the nearest half generation.

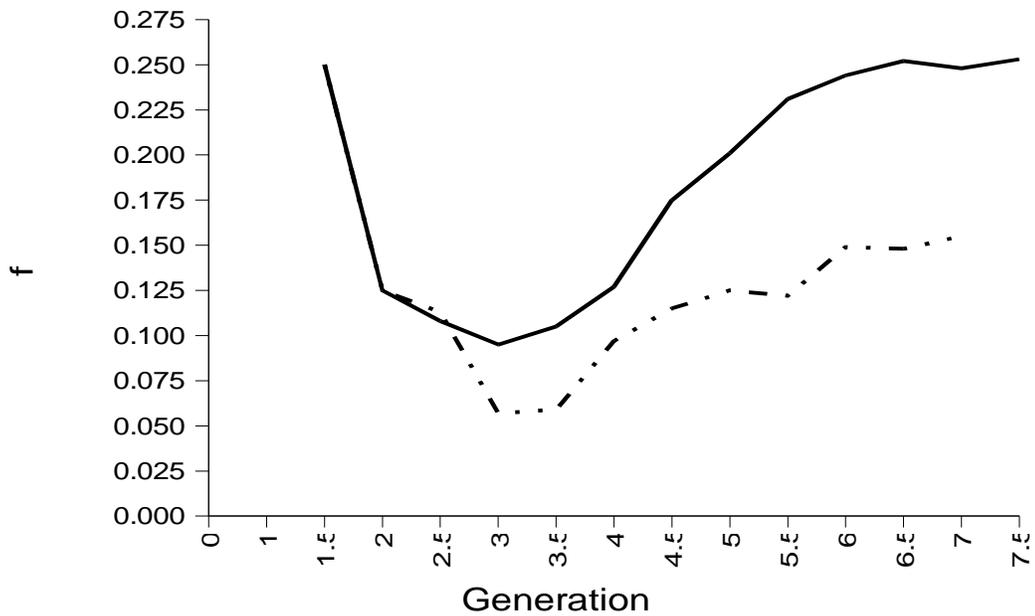
## Results

### Inbreeding and Relationship

Pedigrees were available for all dogs born into the breeding colony since its foundation. As a result, the base population used for the calculation of coefficients of inbreeding and relationship is the actual population of founders. Average and non-zero average coefficients of inbreeding are presented in Figures 3.1 and 3.2, respectively. The average inbreeding in the GS increased rapidly for several generations, and reached a plateau in generation 5.5. The breed average inbreeding has remained steady at  $\approx 25$  percent since generation 6, which is very high. There was a similar rapid increase in inbreeding in the LR population for the first 2.5 generations. There was a decrease in inbreeding between generations 2.5 and 4 which may be attributed to the importation of breeding stock into the populations. After generation 4, there was a continual increase in inbreeding until generation 5.5, and a leveling-off afterward. The level of inbreeding in the LR breed for the past three half-generations has remained steady at  $\approx 15$  percent. Inbreeding has remained constant in both



**Figure 3.1.** Average coefficients of inbreeding for German Shepherds (solid line) and Labrador Retrievers (broken line).

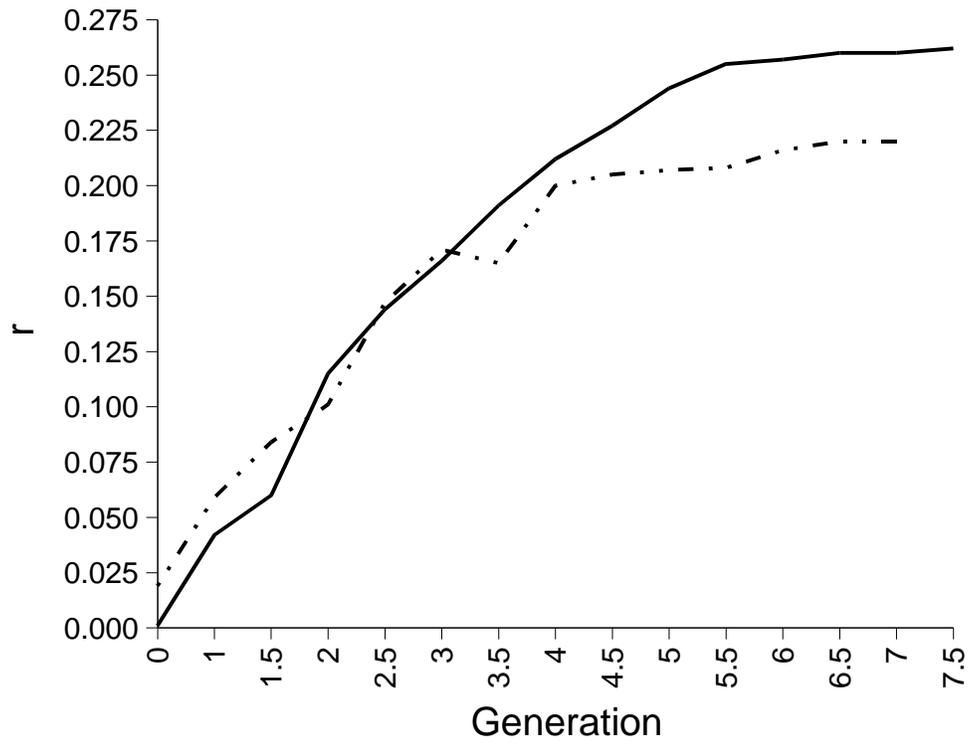


**Figure 3.2.** Average non-zero coefficients of inbreeding for German Shepherds (solid line) and Labrador Retrievers (broken line).

breeds over the past few generations due to changes in management regarding mating decisions.

The results of the non-zero inbreeding analysis are more interesting than those from the whole-population analysis. No inbred individuals were present in either breed until generation 1.5, when single litters of GS and LR pups were produced from son-dam matings. The dramatic decrease in average non-zero inbreeding in generation 2 is due to the increase in the number of inbred individuals and the absence of parent-offspring matings in those generations. In fact, no parent-offspring matings occurred after generation 1.5. For both breeds, the trend in non-zero inbreeding mirrored the trends in breed average inbreeding, steadily increasing each generation after reaching a minimum in generation 3. As the number of inbred animals increased with successive generations, the non-zero average and breed average levels of inbreeding converged. While it appears that the rate of change of inbreeding has neared zero in the last three to four generations, it should be noted that there are fewer litters in the population born in later generations at this time as those generations are still open.

Average pairwise coefficients of relationship are shown in Figure 3.3. The rate of increase in relationship was much higher than that for either measure of inbreeding, and was similar for both breeds until generation 3. Relationships in the GS continued at approximately the same rate, while the rate of increase slowed for the LR. The LR reached a plateau starting with generation 4, while the GS did not reach a similar plateau until generation 5.5. The average pairwise



**Figure 3.3.** Average pairwise relationships for German Shepherds (solid line) and Labrador Retrievers (broken line).

relationships of animals born in generation 7 were  $0.26 \pm 0.004$  (GS) and  $0.22 \pm 0.001$  (LR), which is similar to paternal half-sibs ( $r=0.25$ ). The average pairwise relationship between all animals in the pedigree averaged over all generations were  $0.16 \pm 0.086$  (GS) and  $0.15 \pm 0.063$  (LR). Non-zero pairwise relationships (data not shown) were similar to the average relationships for all generation in both breeds. These relationships are much higher than those reported for national cattle populations. Roughsedge et al. (1999) reported an average pairwise relationship of 0.0134 in British Holsteins born in 1997.

### **Influential Individuals**

A large proportion of the non-zero relationship coefficients in each breed may be attributed to a small number of highly influential sires and dams. The ten most influential sires and dams for each breed were identified based on their average pairwise relationship to the breed in generation 7.5 for the GS and generation 7 for the LR and are presented in Tables 3.1 through 3.4. Complete pedigrees for these animals may be found in Appendices One through Four. Only animals with offspring were considered when identifying influential animals; there are animals with similarly large relationships to their respective breeds which did not produce offspring. As animals with no offspring do not contribute to the genetic structure of the population, they were not of interest for this discussion. Average relationship to the breed was used to identify influential individuals rather than the number of offspring because the former more accurately represents the impact of an individual on the breed at the time of analysis. Contributions to later generations through offspring which become

**Table 3.1.** German Shepherd sires most related to the population.

<b>Sire Name</b>	<b><math>r_{avg}</math></b>	<b>Offspring</b>
Scotty	0.305	277
Thurston	0.277	90
Orbit	0.275	154
Navajo	0.274	56
Stetson	0.273	74
Mercury	0.272	188
Keith	0.269	22
Doug	0.268	23
Varsity	0.267	78
Elgie	0.264	73

**Table 3.2.** German Shepherd dams most related to the population.

<b>Dam Name</b>	<b><math>r_{avg}</math></b>	<b>Offspring</b>
Niki	0.273	13
Bea	0.272	7
Brianna	0.269	19
Fresa	0.269	5
Xandra	0.269	6
Ophelia	0.269	21
Kim	0.269	13
Lori	0.268	26
Gaelic	0.268	27
Lynne	0.267	8

**Table 3.3.** Labrador Retriever sires most related to the population.

<b>Sire Name</b>	<b><math>r_{avg}</math></b>	<b>Offspring</b>
Yale	0.249	66
Scoggins	0.239	106
Doc	0.234	79
Toby	0.230	71
Revere	0.223	70
Quigley	0.222	92
Kaiser	0.222	123
Valiant	0.220	20
Dakota	0.220	54
Burton	0.220	30

**Table 3.4.** Labrador Retriever dams most related to the population.

<b>Dam Name</b>	<b><math>r_{avg}</math></b>	<b>Offspring</b>
Janis	0.229	37
Amber	0.228	33
Fay	0.228	12
Flo	0.228	3
Jamaica	0.228	22
Juniper	0.228	22
Jenny	0.227	8
Belle	0.226	41
Bethany	0.226	39
Pammy	0.224	24

sires and dams of successive generations are also accounted for. The production of a large number of offspring who do not produce offspring of their own does not mark a sire or dam as influential because they do not affect the population in later generations. It was noted that several of the animals producing the most offspring were also selected as most influential by this procedure. Regardless of the procedure used to identify influential ancestors, it is clear that this small group of animals is largely responsible for the magnitude of the average coefficients of inbreeding and relationship currently seen in this population.

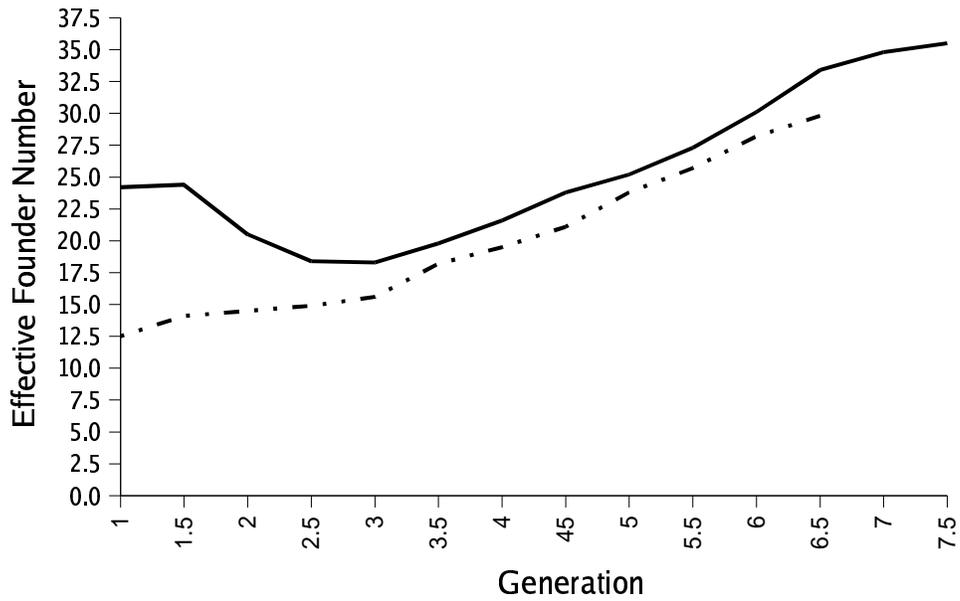
Most of the forty influential ancestors identified had deep pedigrees which extended several generations back to the founders of the breeding colony. The shallowest pedigree was for Kaiser, a fourth-generation LR sire with 123 offspring and an average relationship to the breed of 0.22. The most influential GS sire was Scotty, a fifth-generation animal with 277 offspring and an average relationship to the GS in the colony of 0.305. The GS dams Xandra and Ophelia are eighth-generation paternal half sibs out of Scotty, and possess the shallowest pedigrees among the top GS dams. They have a combined total of 27 offspring and an average relationship of 0.269. The LR dams with the shallowest pedigrees are Belle and Pammy, fifth- and sixth-generation offspring, respectively. Belle is a Kaiser daughter with 41 offspring and average relationship of 0.226. Pammy is a Ryan daughter with 24 offspring and an average relationship of 0.224; Ryan is not a top-ten LR sire. No founders were identified as most-influential ancestors.

A detailed review of the pedigrees in Appendices One through Four will show the extent to which linebreeding has been practiced in this breeding population. Historically some males were retained in the population and used as sires for several female generations with no appreciable restrictions on their use as breeders. That is the origin of most of the lines seen in the pedigrees today. Those lines are maintained because a selection index which weights hip quality and aptitude 2:1 has been used to select candidates for training as guides for several years. Hip dysplasia has a high enough heritability that selection for better-quality hips will favor linebreeding. Research also suggests that various measures of intelligence or aptitude in the dog are also lowly- to moderately heritable.

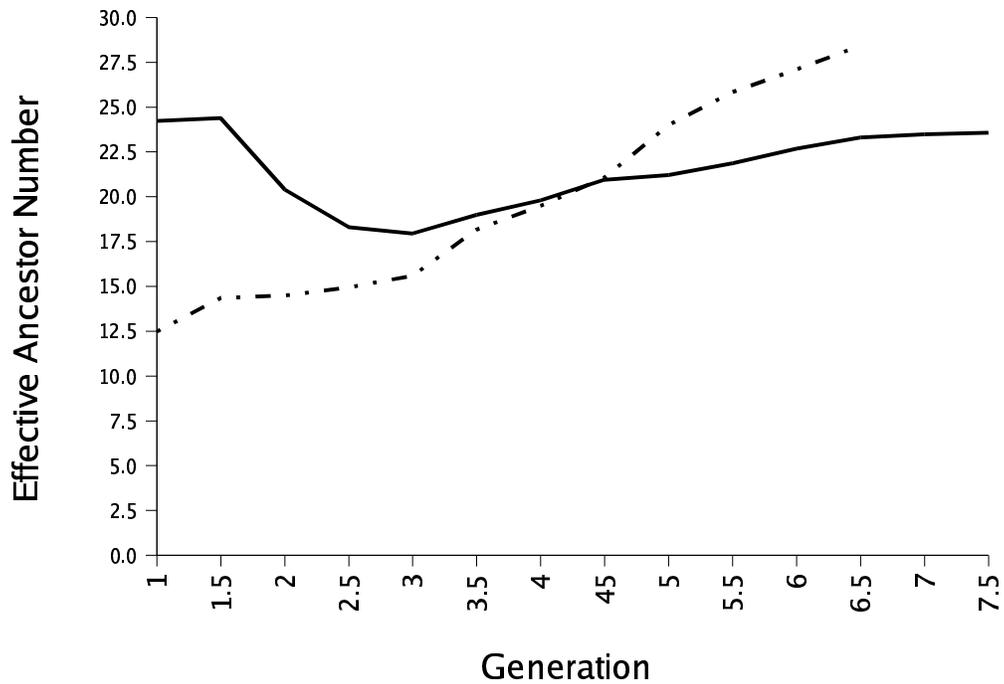
Current selection decisions incorporate limits on the number of matings permitted an individual, as well as the timespan over which animals can be bred. The long-term use of such controls on matings may result in an eventual breakdown of the family lines seen in the pedigrees at the moment, and is certainly a desirable step from the perspective of controlling inbreeding and the loss of alleles from the population.

### **Effective Founder and Ancestor Numbers**

Estimates of  $f_e$  and  $f_a$  for each breed by generation are presented in Figures 3.4 and 3.5. It is clear that while genetic diversity decreased rapidly in the early years of the breeding colony, the rate of decrease has slowed and remained steady for the past several years. The effective ancestor numbers for both breeds were lower than the effective founder numbers, as expected, and



**Figure 3.4.** Effective founder number for German Shepherds (solid line) and Labrador Retrievers (broken line).



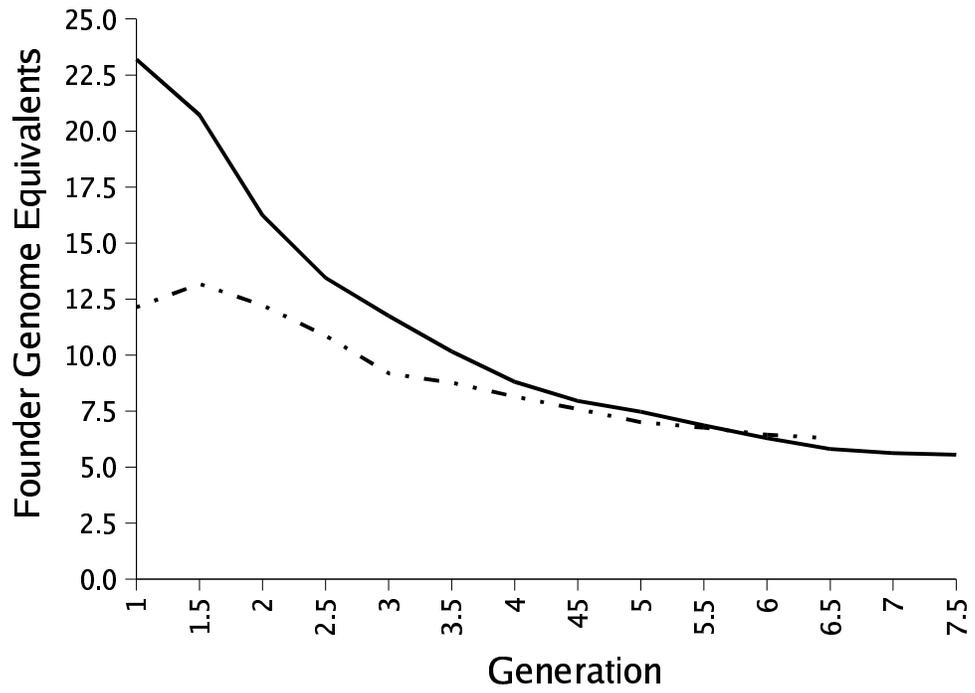
**Figure 3.5.** Effective ancestor number by generation for German Shepherds (solid line) and Labrador Retrievers (broken line),

exhibited a similar trend over time as  $f_e$ . The increase in  $f_a$  in the GS is probably due to changes in management to increase the diversity of the sire and dam portfolio. There was a small increase in  $f_a$  in the GS in 1999 and 2000 which may be due to the influence of five breeders imported between 1994 and 1997. Those five animals collectively produced 96 offspring, although their average relationship to the breed was less than 1 percent.

Counter to expectations, there was an increase in diversity in both breeds as measured by effective founder and ancestor numbers. The use of sires such as Scotty, who was used as a sire for six years and produced 277 pups, and Scotty's grandsire Quasar, who served as a sire for seven years and produced 342 pups, was expected to result in decreases in  $f_e$  and  $f_a$ . In comparison, no LR sire produced more than 245 pups, although five sires did produce 200 or more offspring, and increases in  $f_e$  and  $f_a$  in the LR trailed those in the GS. The observed increase in variability must be due to the continued immigration of parents into both breeds over time. The GS population has always been larger than the LR population, allowing for the use of more sires and dams in that breed, and resulting in an increase in both of these measures of diversity over time.

## **Founder Genome Equivalents**

Estimates of  $f_{ge}$  for each breed by generation are presented in Figure 3.5. The effective founder numbers presented above are not adjusted for loss of genetic variability due to genetic drift over time, and may be biased upwards. In populations which have undergone bottlenecks, genetic drift is an important



**Figure 3.6.** Founder genome equivalents by generation for German Shepherds (solid line) and Labrador Retrievers (broken line).

factor contributing to the loss of diversity. Lacy (1985) showed that

$$f_{ge} \approx N_e / g$$

where  $N_e$  is the effective population size and  $g$  is the generation. Founder genome equivalents should decrease over time, which is consistent with the data in Figure 3.6. There were almost twice as many founders in the GS compared to the LR in generation 0, but there was also a greater loss of diversity in the GS since foundation. Founder genes were lost as a quadratic function of time in the GS and as a linear function of time in the LR. The rate of allele loss has slowed in both breeds in recent years.

### **Generation Interval**

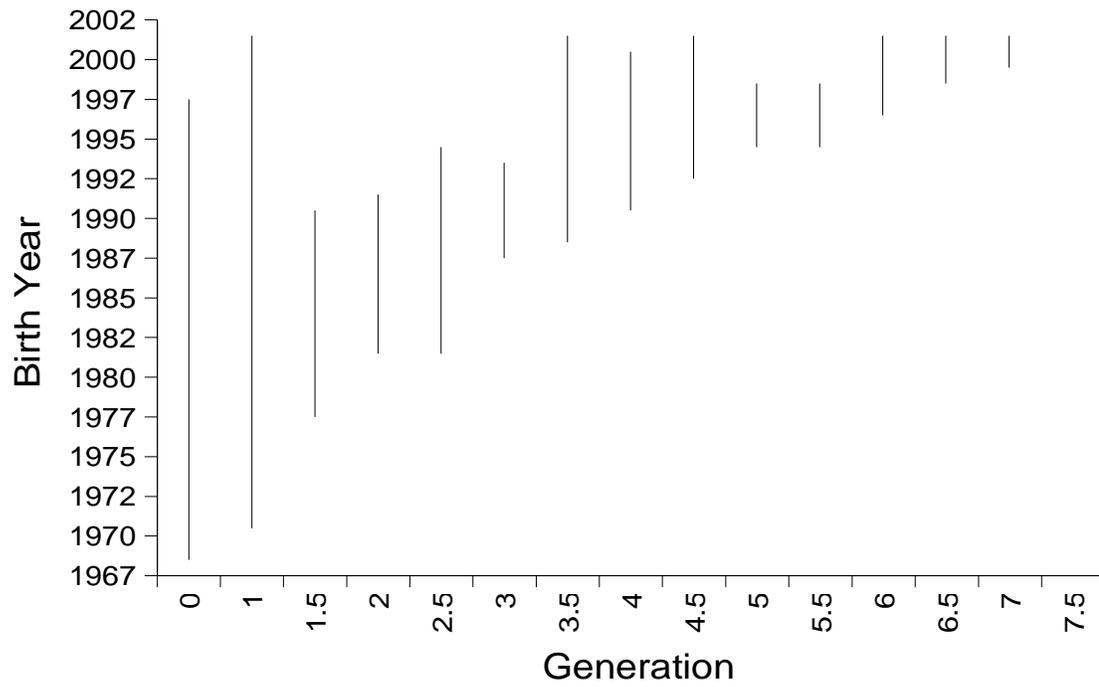
The generation interval is the average age of parents at the time of birth of their selected offspring (Falconer and MacKay, 1996). Overall generation intervals were similar between the two breeds at  $26.56 \pm 0.78$  months for the GS  $25.00 \pm 0.52$  months for the LR. Separate generation intervals were calculated for each sex-breed combination due to the fact that fewer sires than dams were used in the breeding colony. There difference in average generation intervals for German Shepherd sires ( $28.11 \pm 1.90$  months) and dams ( $25.99 \pm 0.81$  months) was not significant. The shortest intervals were similar for males and females, 18.04 versus 16.59 months, and the longest intervals were 97.05 versus 82.33 months, LR sires had a slightly longer average generation interval ( $25.48 \pm 1.81$  months) than dams ( $24.84 \pm 0.35$  months). The range between the shortest and longest intervals for LR sires, 16.26 to 96.39 months, is similar to that of the GS

sires. The range is smaller for the LR dams, 16.46 to 42.35 months, than that for the GS dams.

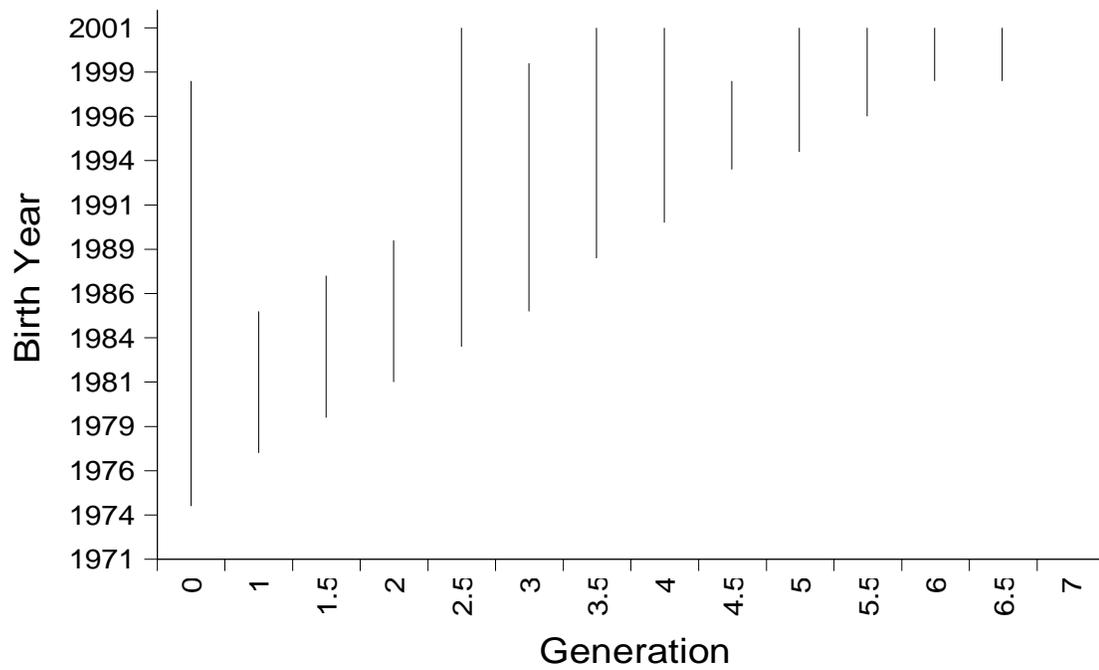
Assuming onset of sexual maturity in the dog at 6 months of age and a 60-day gestation length, the shortest theoretical generation interval in the dog is 8 months, although 12 to 14 months is more probable. The average generation intervals in both breeds and sexes is approximately 24 months, and reflects the health screening and training that dog guides must receive. The use of relatively old dogs as sires and dams reflected in the maxima above is due to the use of animals early in the breeding program for many litters over several half-generations.

## **Demographics**

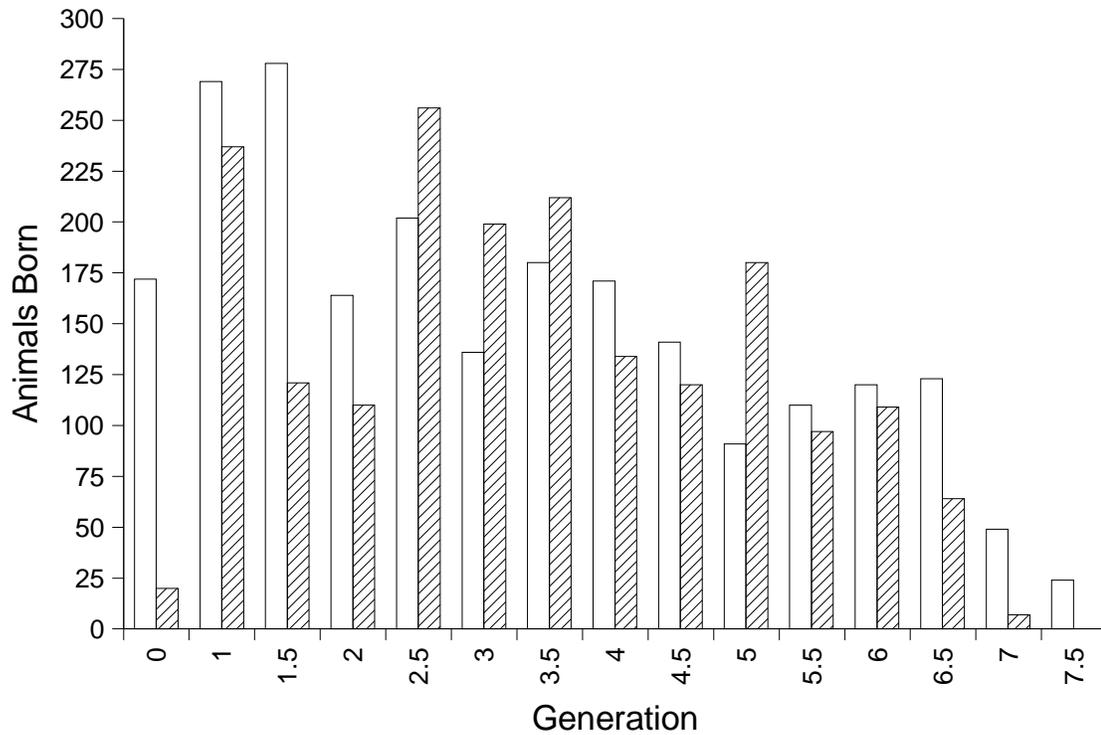
The generation codes used in this study are indicators of the relative amount of selection which has been applied to a group of animals, rather than an absolute measure of distance from the founders of the population. Generations overlap extensively in this population. The birth years spanned by each generation in the GS and LR are presented in Figures 3.7 and 3.8, respectively. In the GS, generations 0 and 1 spanned long periods of time, while successive generations spanned much shorter periods. In the LR, early generations were relatively short, spanning about eight birth years per generation, while later generations tend to span a larger period of time. There is considerable variation in generation length for both breeds. The majority of the most influential sires and dams in each breed (Tables 3.1 through 3.4) were born in generations 4+. Short generations are indicative of rapid replacement of breeding stock. Patterns



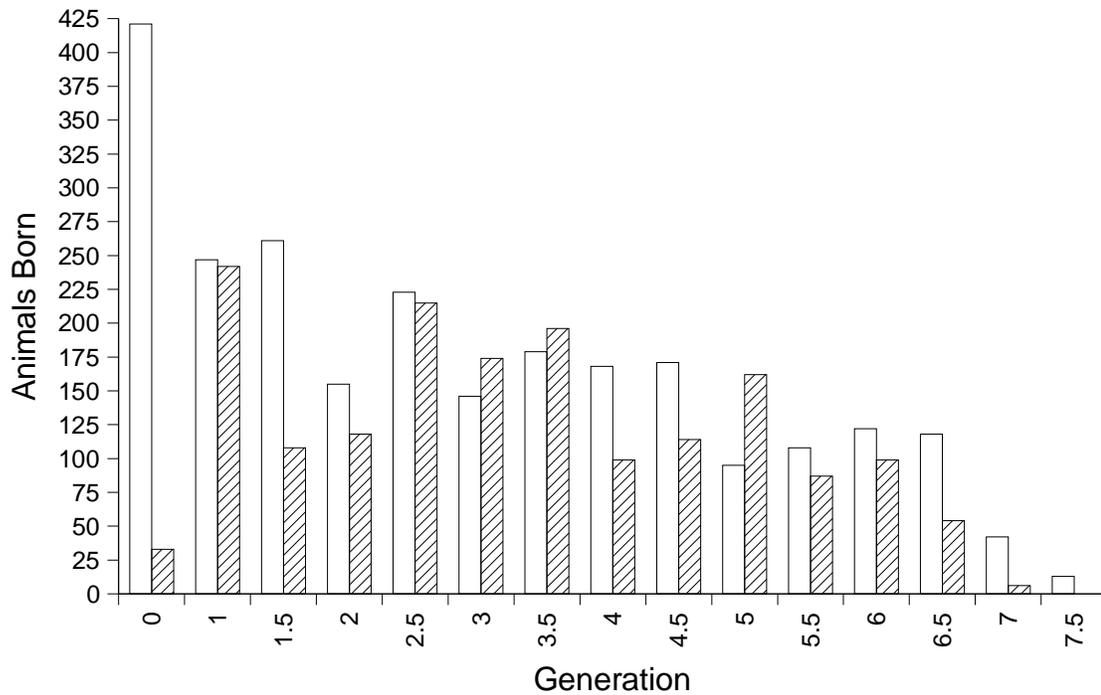
**Figure 3.7.** Birthyears spanned by generations (German Shepherds).



**Figure 3.8.** Birthyears spanned by generations (Labrador Retrievers).



**Figure 3.9.** German Shepherds births by generation for males (unfilled) and females (hatched).

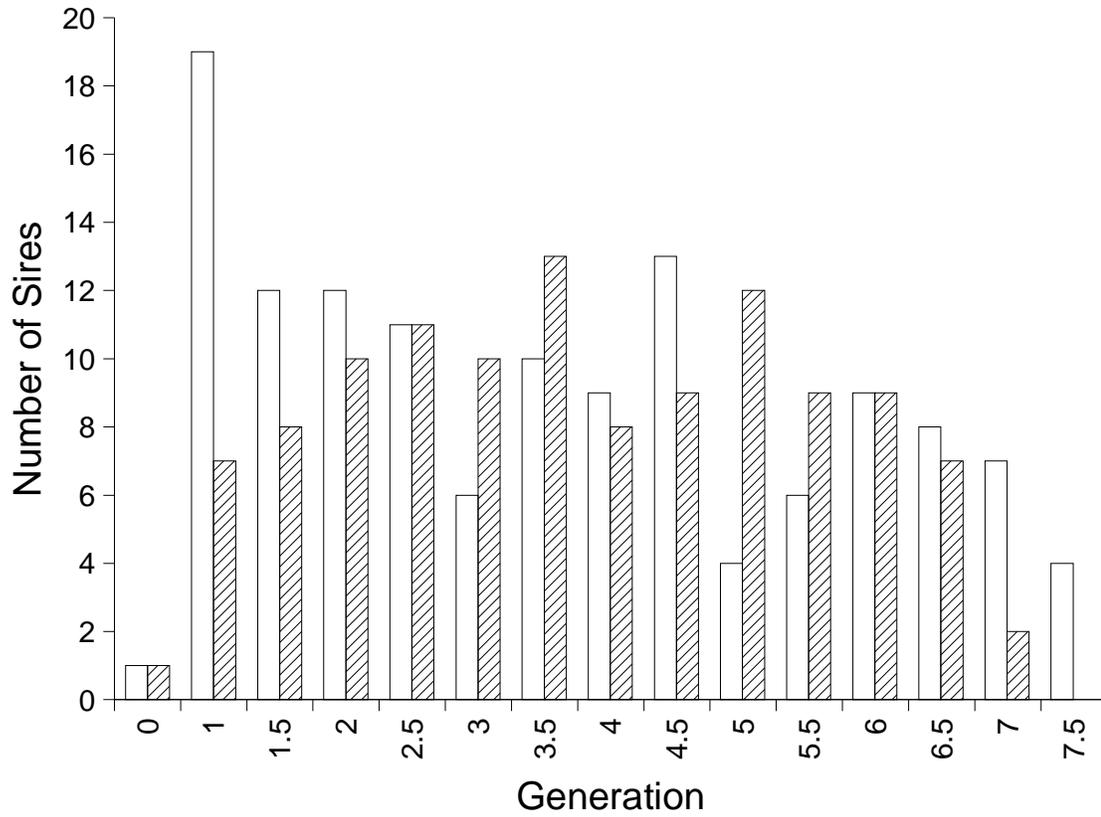


**Figure 3.10.** Labrador Retriever births by generation for males (unfilled) and females (hatched).

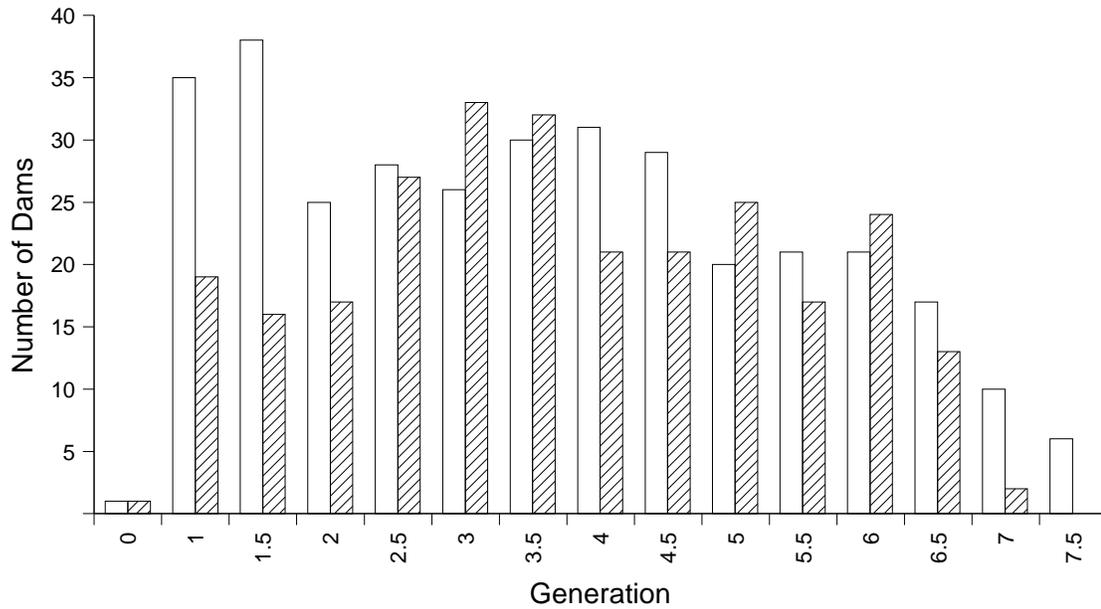
were similar for both breeds. Generation 0 consists of all animals with unknown parents, and as long as there is migration of new breeding stock into the breeding colony that generation will span all birth years in the population.

Births by sex for each breed are presented in Figures 3.9 and 3.10. The sex ratio (West et al., 2002) varies slightly from generation to generation, but over time remains approximately 50:50 in the GS (48:52) and LR (52:48). There is a large apparent deviation from this ratio in favor of sires in generation 0, but this is only because all founders are placed into that generation. More males than females are represented in generation 0 because many founder males were mated to females produced within the breeding colony. The number of births appears to decrease in the later generations. This is due to the fact that generations overlap birth years extensively and there will be animals born into the later generations in Figures 3.7 and 3.8 for several more years. There will not be a decrease in total births in later generations unless there is a change in the number of animals required by The Seeing Eye.

A downward trend similar to that for births by generation is noted for the number of sires and dams used per generation (Figures 3.11 and 3.12). As would be expected, more dams than sires were used each generation (approximately 2:1). It is interesting to note that this represents a much more equitable distribution of selection intensity between the two sexes than is typically the case in livestock breeding. This disparity is usually due to the fact that males can produce large numbers of offspring relative to females. Litter-bearing females are able to contribute a larger number of offspring to the population than

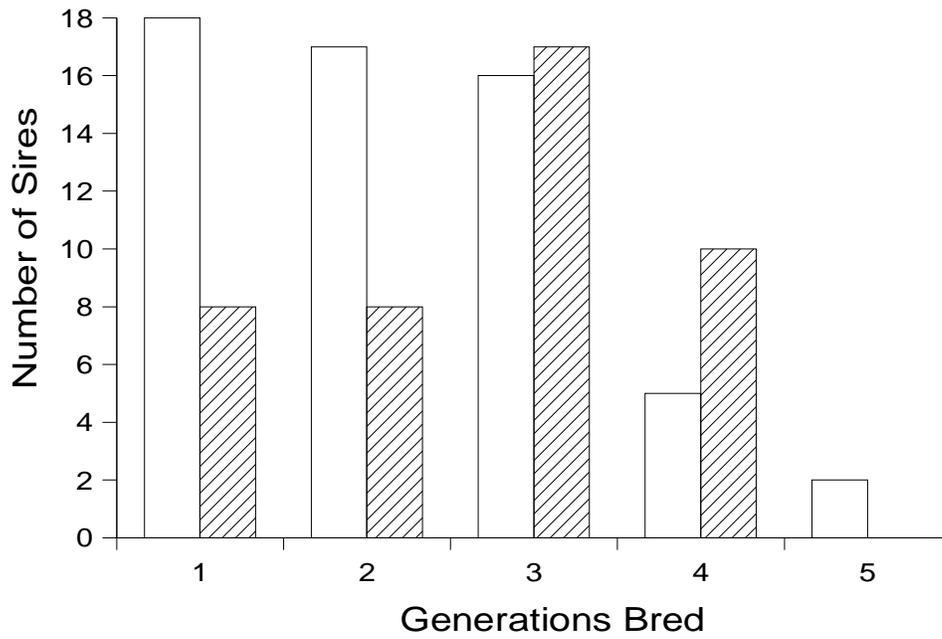


**Figure 3.11.** Sires used by generation for German Shepherds (unfilled) and Labrador Retrievers (hatched).

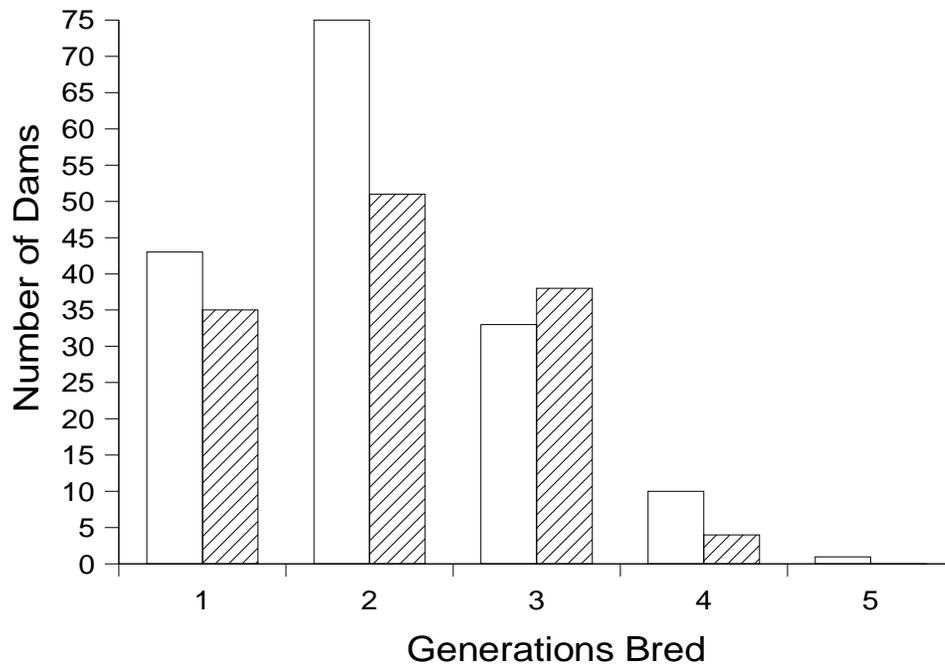


**Figure 3.12.** Dams used by generation for German Shepherds (unfilled) and Labrador Retrievers (hatched).

non-litter-bearing females, but while several dams in each breed had more than 50 offspring, no dams produced more than 100 offspring. The ten sires in each breed who produced the most offspring had more than 100 pups in every case. GS sires produced an average of  $70.79 \pm 9.83$  offspring, while GS dams produced an average of  $25.35 \pm 1.29$  offspring. LR sires produced an average of  $81.86 \pm 9.63$  offspring, while LR dams produced an average of  $27.50 \pm 1.54$  offspring. Labrador Retriever and GS sires had similar but not significantly different ( $P > 0.05$ ) tenures,  $2.67 \pm 1.04$  versus  $2.24 \pm 1.09$  generations, while there was no difference ( $P > 0.05$ ) between LR and GS dams,  $2.09 \pm 0.83$  versus  $2.08 \pm 0.88$  generations. There was no significant difference ( $P > 0.05$ ) between the average number of litters produced by GS and LR sires,  $11.18 \pm 1.59$  versus  $12.23 \pm 1.87$ . German Shepherd and LR dams produced  $\approx 1/3$  as many litters on average as sires,  $3.99 \pm 0.18$  and  $4.11 \pm 0.36$ . There was no significant difference ( $P > 0.05$ ) between breeds for litters produced per dam. The distribution of generations bred for sires (Figure 3.13) shows that sires overlapped generations, that is, sires were able to produce offspring in more than one generation. No LR sire produced litters in more than 4 distinct generations, and no GS sire in more than 5 distinct generations. German Shepherd and LR dams were similarly able to produce offspring in more than one distinct generation (Figure 3.14); most dams produced litters in 1 to 3 generations, while only four LR dams produced litters in 4 generations and only one GS dam in 5 generations.



**Figure 3.13.** Sire service life in generations for German Shepherds (unfilled) and Labrador Retrievers (hatched).



**Figure 3.14.** Dam service life in generations for German Shepherds (unfilled) and Labrador Retrievers (hatched).

A total of 58 GS sires and 162 GS dams produced 4,106 offspring in 647 litters ( $5.06 \pm 0.24$  pups/litter) while 43 LR sires and 128 LR dams produced 3,520 offspring in 527 litters ( $7.37 \pm 0.17$  pups/litter). There was a difference ( $P < 0.05$ ) between the two breeds with respect to litter size.

These results describe a population that is in relatively good health from a genetic perspective. While non-zero coefficients of relationship and average pairwise relationships increased dramatically for several generations, that rate of increase has slowed almost to zero. Effective founder and ancestor numbers indicate that diversity in the population has increased slightly since the founding of the breeding colony, and is probably due to the periodic migration of unrelated breeding stock into the colony. The rate of allele loss as measured by founder genome equivalents has also slowed to near zero, indicating that allelic diversity is being maintained near a steady state in the population.

Generation intervals are averaging approximately twenty-four months in both breeds, and while it would be desirable to select sires at a younger age from a theoretical perspective, is not practical in this case due to the intense selection for health and aptitude practiced in this particular colony. However, the relatively short generation intervals, in concert with good screening, has probably contributed to the excellent hip quality seen in these dogs (Leighton, 1997). The number of sires and dams used each generation, as well as the number of puppies whelped, has remained fairly constant over time. This reflects demand for dog guides, resources available for raising and training puppies, and resources available for matching and training dogs and handlers. The high, non-

recoverable cost of producing dog guides also contributes to this. Sire and dam service lives are reasonably short and reflect the availability of new breeding stock. Current management practices should be maintained, notably the periodic immigration of breeding stock.

The most likely sources of such individuals are other organizations, such as Guiding Eyes for the Blind, Inc. or Guide Dogs for the Blind, Inc., which also breed dogs for use as guides. While they may not use identical selection criteria to The Seeing Eye, Inc., they do use more rigorous selection criteria than the average purebred dog breeder (E. A. Leighton, personal communication). In cases where hip scores and distraction indices are available for potential immigrants, the selection index score used by The Seeing Eye, Inc., can be constructed directly. In other cases, those scores can be obtained at relatively low cost. It is difficult to consider circumstances under which the use of commercial breeder-produced animals would be recommended; the loss of selection pressure for hip quality and aptitude which would result are unacceptable.

## **CHAPTER 4**

# **GENETIC PARAMETERS AND BREEDING VALUES FOR PRODUCTIVE LIFE IN GERMAN SHEPHERD AND LABRADOR RETRIEVER DOG GUIDES**

### **Introduction**

The cost of replacing a dog guide is high both financially and emotionally. High mortality rates result in high operating costs, aversion to dog guide use, and caution on the part of financial backers. Clearly it is to the advantage of all parties involved with dog guides to minimize animal mortality and maximize working life.

The aims of this part of the study are the development of a model for genetic analysis of working life; the estimation of direct and indirect genetic variance components for working life in a colony of dog guides; and the estimation of animal breeding values..

### **Materials and Methods**

#### **Data**

Data were provided by The Seeing Eye, Inc. of Morristown, NJ, and consisted of records from 1,403 German Shepherd (GS) and 1,814 Labrador Retrievers (LR) used as guides for blind people. For each dog, the data set included gender, date of birth, unique litter ID, date of graduation from training, date of retirement, reason for retirement, parity, handler gender, handler age, coefficient of inbreeding, and number of days worked as a guide. Records were coded as censored when a dog ended its working life prematurely, i.e., when its

handler was unable to continue using the dog as a guide due to a health or temperament problem on the part of the dog. Records were also coded as censored if a dog died from accidental causes, such as a house fire. Based on notes in the data file, dogs were placed into one of six classes based on their reason for retirement. Descriptions and counts for each class by breed are presented in Tables 4.1 and 4.2. Only dogs which served as guides for a single handler were included in the dataset. The trait of interest in this study was length of working life. Working life was initially defined as the length of time, in days, between a dog's graduation from training and that dog's retirement.

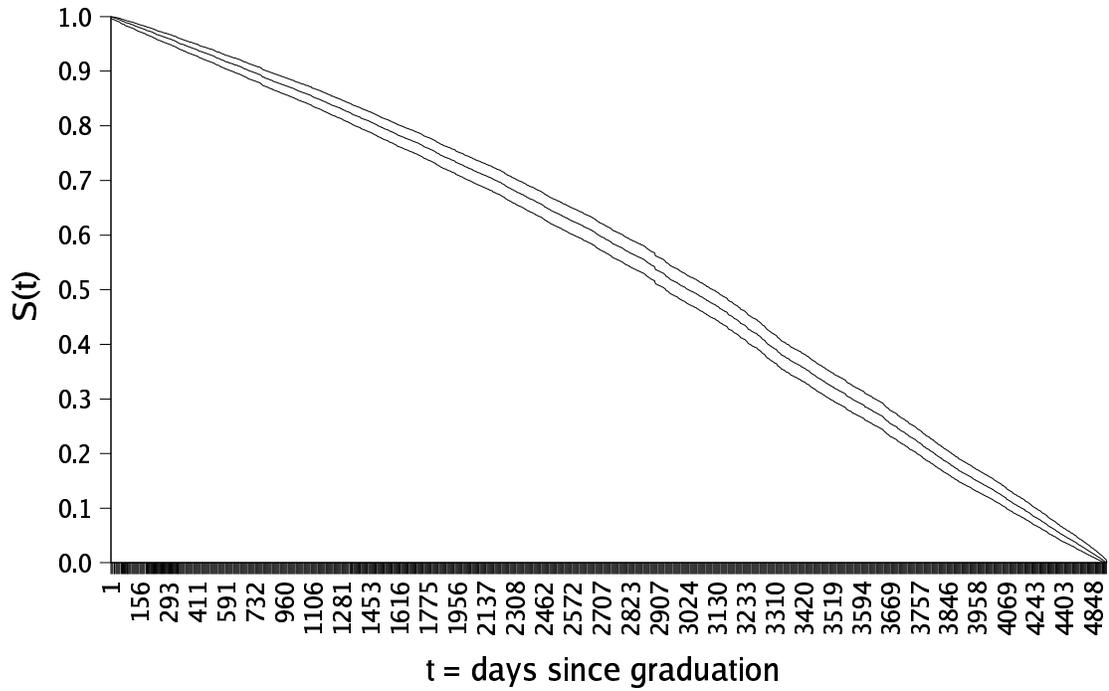
The Kaplan-Meier estimate,  $S_{KM}(t)$ , of the survival curves for GS and LR are presented in Figures 4.1 and 4.3, respectively. The survival curves are reasonably smooth over the range of the data. However, a plot of  $\ln(-\ln(S_{KM}(t)))$  versus  $\ln(t)$  for GS (Figure 4.2) suggests that mortality rates or censoring mechanisms were different before and after 540 days (i.e.,  $\ln(t) \sim 6.29$ ) of working life. The latter explanation is more reasonable given that Figure 4.2 does not show a noticeable change in mortality at that time. Figure 4.4 shows the plot of  $\ln(-\ln(S_{KM}(t)))$  for LR, which is also notably non-linear over a similar timespan. In such cases, Ducrocq et al. (2000) recommend defining separate measures of working life that correspond to different phases of the production- or life-cycle. Based on the change of slopes in Figures 4.2 and 4.4, two separate measures of working life were defined: early working life, from 0 to 180 days (EWL); and later working life, from 181 days until retirement (LWL). Early and later working life were calculated for both breeds and used as the basis for this

**Table 4.1** Number of German Shepherds in each retirement class.

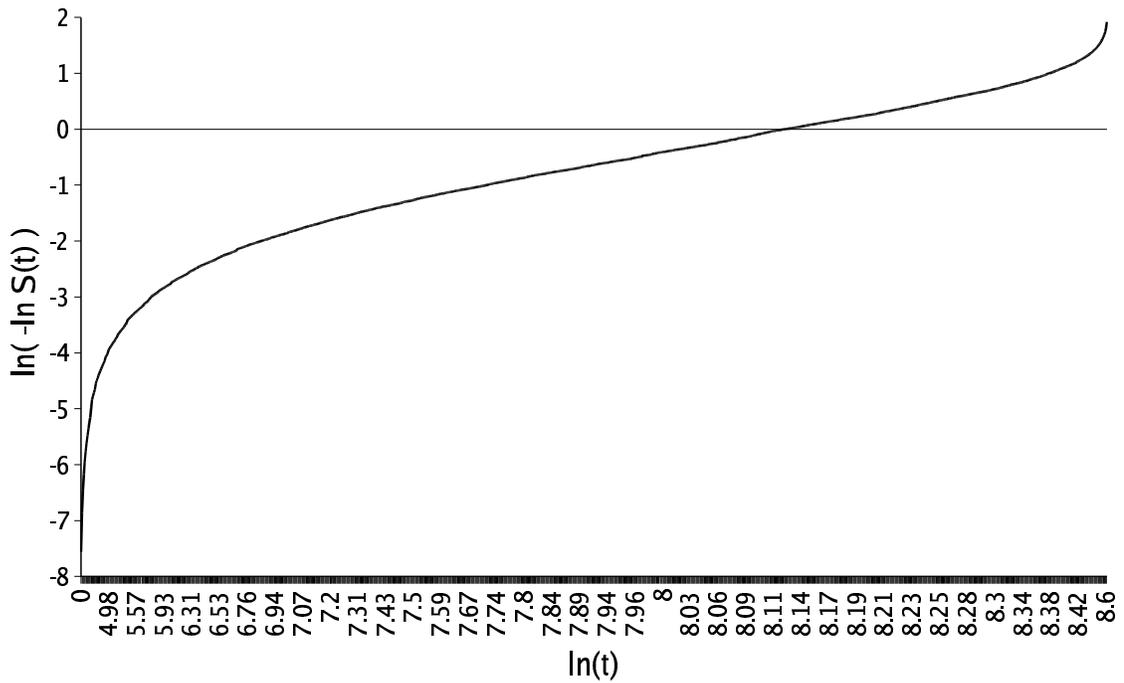
<b>Retirement Class</b>	<b>Description</b>	<b>N</b>
1	Retired due to health/injury.	503
2	Retired, no reason given.	41
3	Retired due to behavioral problems.	169
4	Retired due to problems with handler.	102
5	No notation in records as to current status.	168
6	Animal censored, not retired.	420

**Table 4.2.** Number of Labrador Retrievers in each retirement class.

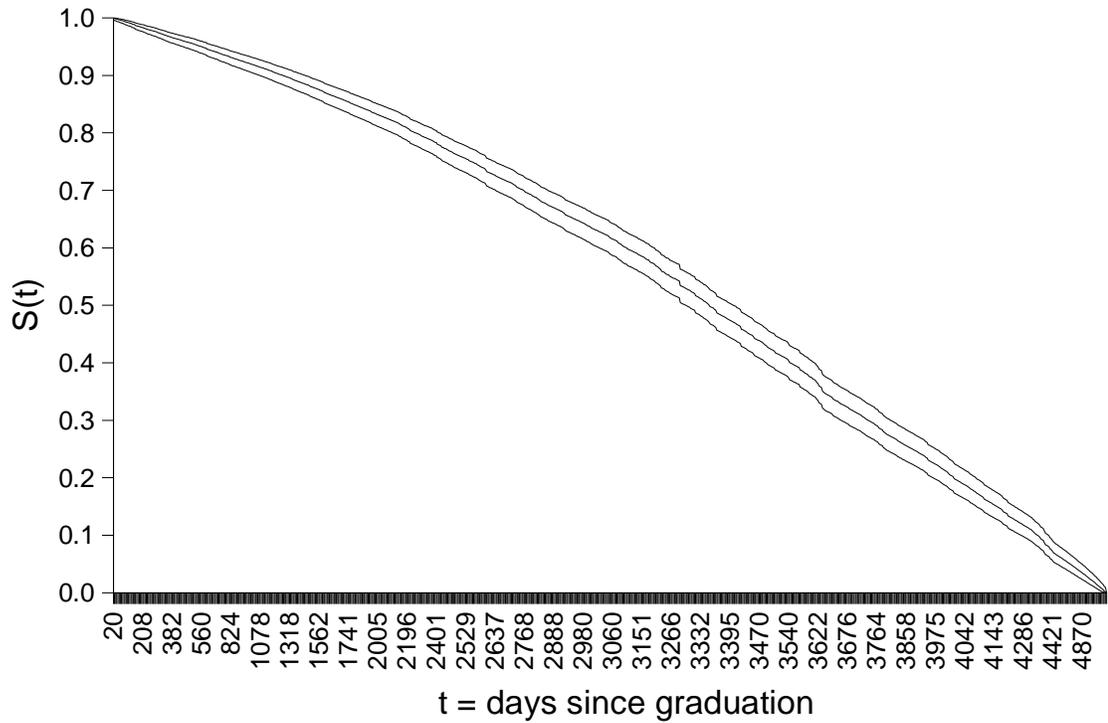
<b>Retirement Class</b>	<b>Description</b>	<b>N</b>
1	Retired due to health/injury.	677
2	Retired, no reason given.	29
3	Retired due to behavioral problems.	95
4	Retired due to problems with handler.	178
5	No notation in records as to current status.	287
6	Animal censored, not retired.	548



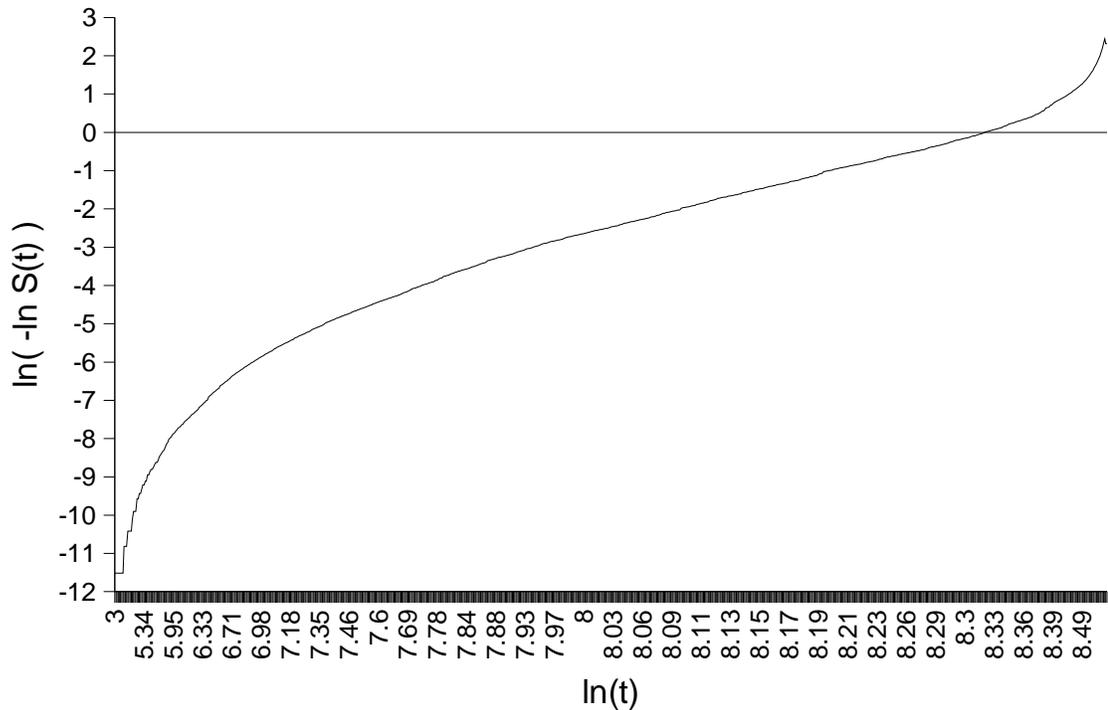
**Figure 4.1.** Nonparametric Kaplan-Meier estimate (95% confidence interval) of the German Shepherd survival curve.



**Figure 4.2.** Graphical test of the assumption that the baseline hazard function for the German Shepherd population follows a Weibull model.



**Figure 4.3.** Nonparametric Kaplan-Meier estimate (95% confidence interval) of the Labrador Retriever survival curve.



**Figure 4.4.** Graphical test of the assumption that the baseline hazard function for the Labrador Retriever population follows a Weibull model.

analysis. Figures 4.5 and 4.6 show the distribution of actual working life in GS and LR, respectively. There is a clear bimodal distribution of working life in LR, and working life in GS is also non-normal.

## Analysis

The model used to analyze early and late working life was:

$$\lambda(t) = \lambda_0(t) \exp[ dg_i + by_j + l_k + rc_l + p_m + ha_n + hg_o + s_p + f ]$$

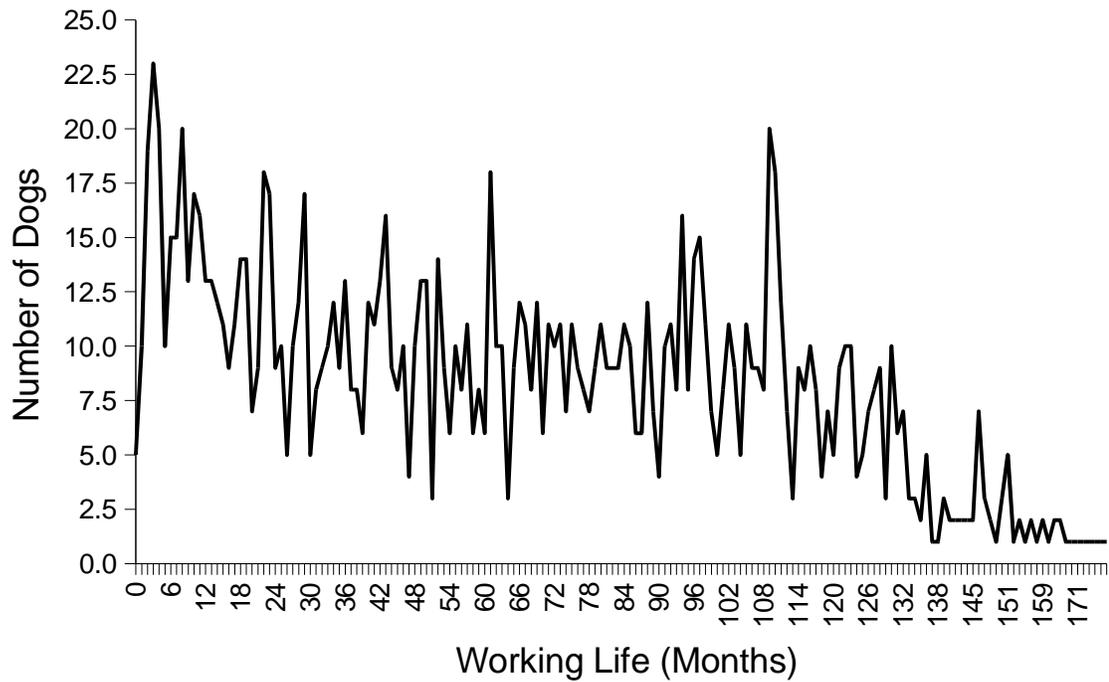
where  $\lambda(t)$  = the hazard function at time  $t$ ;  $\lambda_0(t) = \lambda\rho(\lambda t)^{\rho-1}$  = a Weibull baseline hazard function with shape and scale parameters  $\rho$  and  $\lambda$ , respectively;  $dg_i$  = fixed effect of animal gender  $i$ ;  $by_j$  = fixed effect of birth year  $j$ ;  $l_k$  = fixed effect of litter  $k$ ;  $rc_l$  = fixed effect of retirement class  $l$ ;  $p_m$  = fixed effect of parity  $m$ ;  $ha_n$  = fixed effect of handler age  $n$ ;  $hg_o$  = fixed effect of handler gender  $o$ ;  $sire_k$  = random effect of sire  $k$ ; and  $inbr$  = inbreeding fit as a covariate.

In order to calculate a linear-scale estimate of heritability for working life, an estimate of the loggamma parameter,  $\gamma_{BY}$ , for birth year was required.

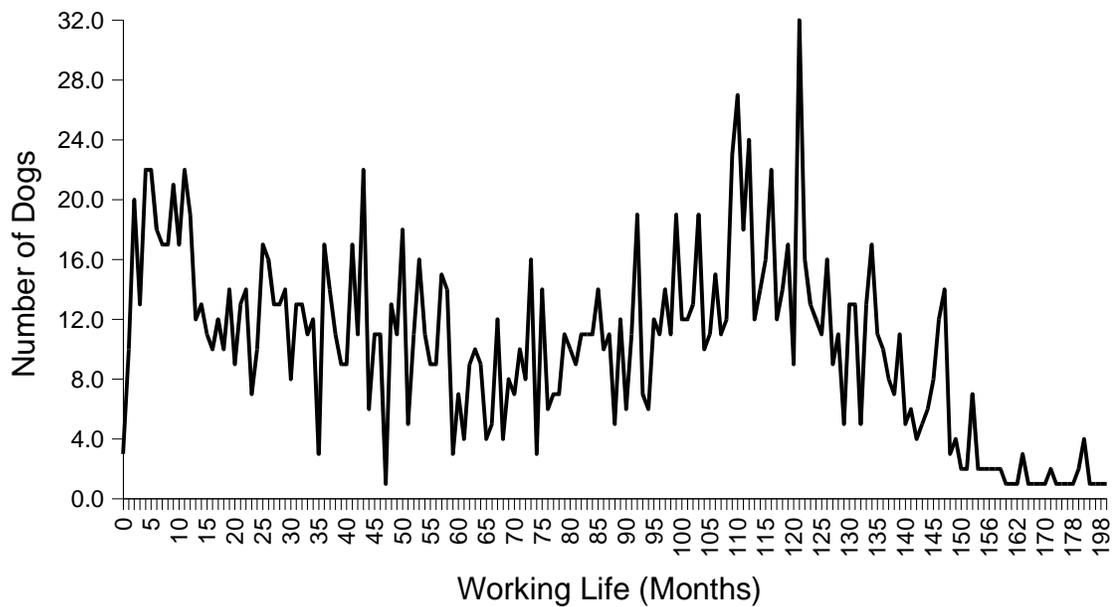
The model used to estimate this parameter was:

$$\lambda(t) = \lambda_0(t) \exp[ dg_i + by_j + l_k + rc_l + p_m + ha_n + hg_o + s_p + f ]$$

This differs from the previous model only in that  $by_j$  = the loggamma-distributed random effect of birth year  $j$ . The parameter  $\gamma_{BY}$  was estimated jointly with the other effects. All attempts fit a Weibull model failed to converge, with estimates of  $\gamma_{BY}$  tending to  $+\infty$ . This may be due to the large number of fixed-effects classes relative to the number of observations available for analysis. A Cox model, which is more computationally demanding but more generalized, was



**Figure 4.5.** Distribution of working life (months) for German Shepherds.



**Figure 4.6.** Distribution of working life (months) for Labrador Retrievers.

successfully used to fit this model. Once an estimate of  $\gamma_{BY}$  was obtained, this model was discarded and not used for the remainder of the analyses.

## **Parameter Estimation**

The Survival Kit V3.12 software package (Ducrocq and Sölkner, 1994; Ducrocq and Sölkner, 1998) was used to fit the Cox and Weibull models described above. The random effect of sire for each trait was fit with a multivariate normal density function with (co)variances derived from genetic relationships defined in the pedigree file. Only sire information was included in the pedigree files and pedigrees were complete back to the founding of the population. As there is no reason to believe that selection for working life as a dog guide was practiced in either breed prior to the establishment of TSEI's breeding colony, no genetic groups (Westell et al., 1988) were defined.

A large-sample likelihood ratio test was used to assess the influence of the fixed effects in the model. Twice the change in the log-likelihood from including a new effect in the model was compared to a Chi-squared distribution with degrees of freedom equal to the number of estimable levels of the new effect. The log-likelihood ratio was formed by comparing the full model with models excluding one factor at a time, which is similar to Type III sums-of-squares in the traditional linear model.

## **Results**

### **Censoring**

The number and percentage of censored records are presented by trait and breed in Table 4.3. Summary statistics for censoring time are presented

in Table 4.4. Censoring was extreme for EWL in both breeds, but was much more moderate for LWL. Censoring rates were similar between breeds for EWL, but there was a difference of 15.6% between GS and LR for LWL. The average censoring time for LWL in GS was 832.22 d versus 1931.27 d for LR. German Shepherds records were censored more heavily than LR, and at younger ages. Maximum censoring times for EWL were 541 d in GS and LR, and were 4972 d and 4781 d for LWL.

### **Fixed Effects**

Tables 4.4-4.8 show the likelihood ratio tests of fixed effects for EWL and LWL in GS and LR, respectively. Virtually all tests were significant at  $P < 0.10$  for both traits in both breeds, with the exception of sex and birth year for LWL in GS. In all cases, inbreeding had a negative slope, but the slopes were not significantly different from zero ( $P > 0.10$ ). Given the size of the datasets in this study, it is unlikely that the tests of significance reflect differences with small actual magnitudes as is the case with extremely large datasets.

The exponential of estimates for levels of fixed effects may be viewed as relative culling risks and plotted for easy interpretation (Beaudeau et al., 1995). If the relative culling risk for a class of fixed effects is 2, an animal in that class is twice as likely to be culled as an animal in the reference class. Reference classes have a relative culling ratio of 1. For some levels of fixed effects, the relative risks were very large, which resulted in an undesirable smoothing of the graph. In the figures that follow which present relative culling risks, the maximum risk has usually been rounded to 20 or 25. This is a large

**Table 4.3.** Number (percent) of censored records by trait and breed.

<b>Trait</b>	<b>Breed</b>	<b>N Censored</b>	<b>% Censored</b>	<b>N</b>
EWL	GS	1297	92.45	1403
	LR	1732	95.48	1814
LWL	GS	672	47.90	1403
	LR	586	32.30	1814

**Table 4.4.** Summary statistics for censoring time (days) by trait and breed.

<b>Trait</b>	<b>Breed</b>	<b>Average</b>	<b>Min</b>	<b>Max</b>
EWL	GS	506.28	5	541
	LR	2322.80	11	541
LWL	GS	832.33	2	4972
	LR	1931.27	1	4781

**Table 4.5.** Results from likelihood ratio tests comparing the full model for Early Working Life in German Shepherds with models excluding one effect at a time.

<b>Effect</b>	<b>df</b>	<b>-2Δ log-likelihood<sup>1</sup></b>	<b>Prob<sup>2</sup></b>
Gender	1	886.59	>0.10
Birthyear	22	902.36	>0.10
Litter	91	1232.63	<0.01
Retirement class	5	1068.14	<0.01
Parity	9	897.53	<0.10
Handler age	40	1016.19	<0.01
Handler gender	1	895.29	>0.10
Inbreeding	1	897.96	>0.10

<sup>1</sup>Logarithm of the marginal posterior odds ratio at the posterior mode.

<sup>2</sup>Probability of observing a change of such magnitude in the log-likelihood ratio strictly by chance.

**Table 4.6.** Results from likelihood ratio tests comparing the full model for Late Working Life in German Shepherds with models excluding one effect at a time.

<b>Effect</b>	<b>df</b>	<b>-2Δ log-likelihood<sup>1</sup></b>	<b>Prob<sup>2</sup></b>
Gender	1	9959.09	<0.01
Birthyear	24	10230.28	<0.01
Litter	358	10478.70	<0.01
Retirement class	5	9880.91	<0.01
Parity	10	7287.47	<0.01
Handler age	64	8381.14	<0.01
Handler gender	1	8465.70	<0.01
Inbreeding	1	10073.61	<0.01

<sup>1</sup>Logarithm of the marginal posterior odds ratio at the posterior mode.

<sup>2</sup>Probability of observing a change of such magnitude in the log-likelihood ratio strictly by chance.

**Table 4.7.** Results from likelihood ratio tests comparing the full model for Early Working Life in Labrador Retrievers with models excluding one effect at a time.

<b>Effect</b>	<b>df</b>	<b>-2Δ log-likelihood<sup>1</sup></b>	<b>Prob<sup>2</sup></b>
Gender	1	440.47	<0.01
Birthyear	22	499.30	<0.01
Litter	66	751.49	<0.01
Retirement class	4	773.17	<0.01
Parity	9	453.70	<0.01
Handler age	38	572.92	<0.01
Handler gender	1	429.55	<0.05
Inbreeding	1	437.74	<0.01

<sup>1</sup>Logarithm of the marginal posterior odds ratio at the posterior mode.

<sup>2</sup>Probability of observing a change of such magnitude in the log-likelihood ratio strictly by chance.

**Table 4.8.** Results from likelihood ratio tests comparing the full model for Late Working Life in Labrador Retrievers with models excluding one effect at a time.

<b>Effect</b>	<b>df</b>	<b>-2Δ log-likelihood<sup>1</sup></b>	<b>Prob<sup>2</sup></b>
Gender	1	18327.17	<0.01
Birthyear	24	18854.45	<0.01
Litter	307	19001.76	<0.01
Retirement class	5	19398.37	<0.01
Parity	10	18399.10	<0.01
Handler age	65	18454.59	<0.01
Handler gender	1	18383.61	<0.01
Inbreeding	1	18379.72	<0.01

<sup>1</sup>Logarithm of the marginal posterior odds ratio at the posterior mode.

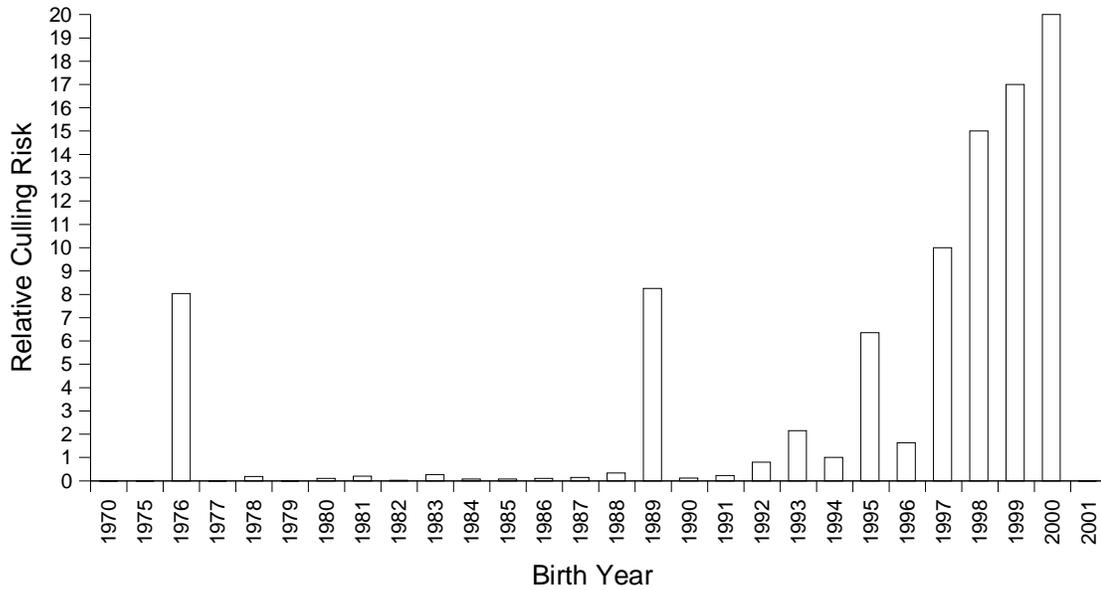
<sup>2</sup>Probability of observing a change of such magnitude in the log-likelihood ratio strictly by chance.

enough value to represent large changes in relative risks while allowing smaller changes to be noted.

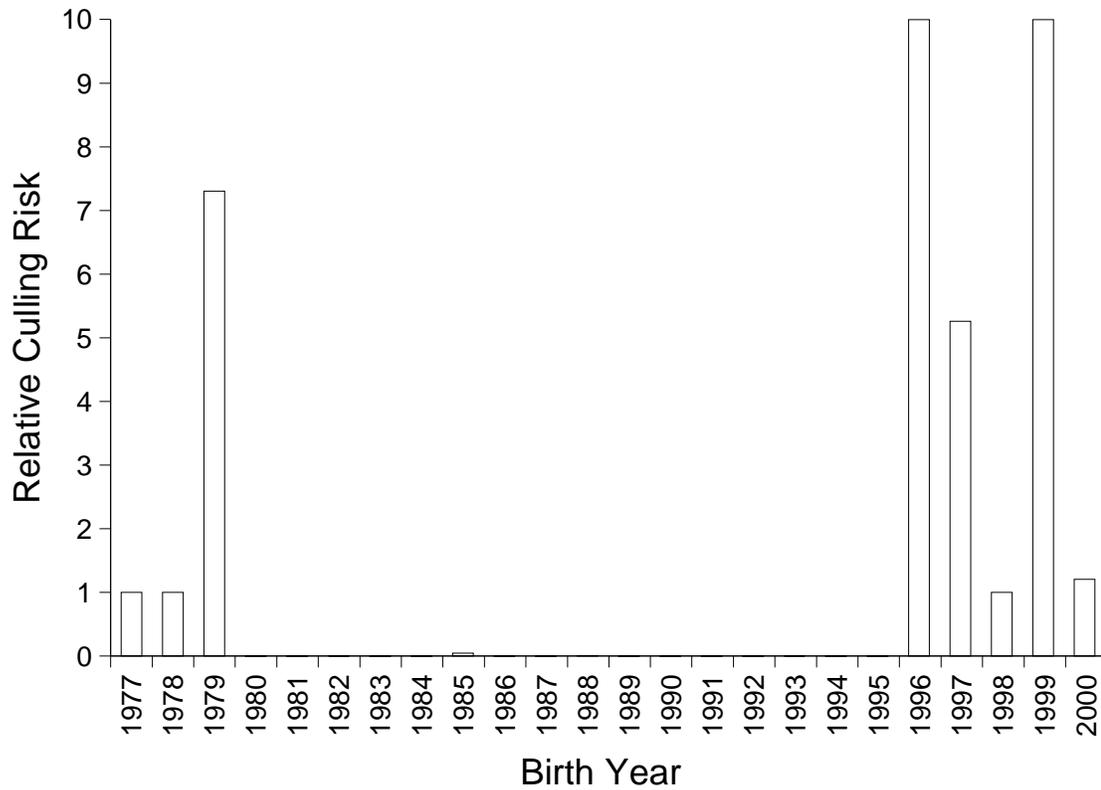
## **Early Working Life**

Female GS dog guides were only 0.66 times as likely to be culled as males. This is consistent with observations that males are more aggressive than females, and that more GS than LR must be screened to find an animal with a suitable temperament for guide work (E. Leighton, 2002, personal communication). Similarly, female LR were only 0.53 times as likely to be culled as male LR.

Figures 4.7 and 4.8 display relative culling risks for birth year in GS and LR, respectively. For GS, the risks were relatively constant, with peaks in 1976 and 1989, until 1992, when there was a sharp increase in risk until 2001. The high risk in 1976 corresponds to a time period when a large number of dogs were brought into the training program, and represents the culling of imported animals not well-suited for use as guides. For LR, the risks were constant until 2001, when there was a sharp increase in risk. Rather than reflecting a biological or management process, the large increases in risk in later birth years were artifacts of the estimation procedure. There were few individuals born in those years that have worked as guides; as a result, the estimates for those levels of the birth year fixed effect were poor, with large associated standard errors. Significant litter effects were found for both breeds. Risks were not plotted and compared as such a comparison does not have a clear interpretation. Litter differences may represent differences in maternal ability.



**Figure 4.7.** Estimates of the birth year effect for Early Working Life in German Shepherds.

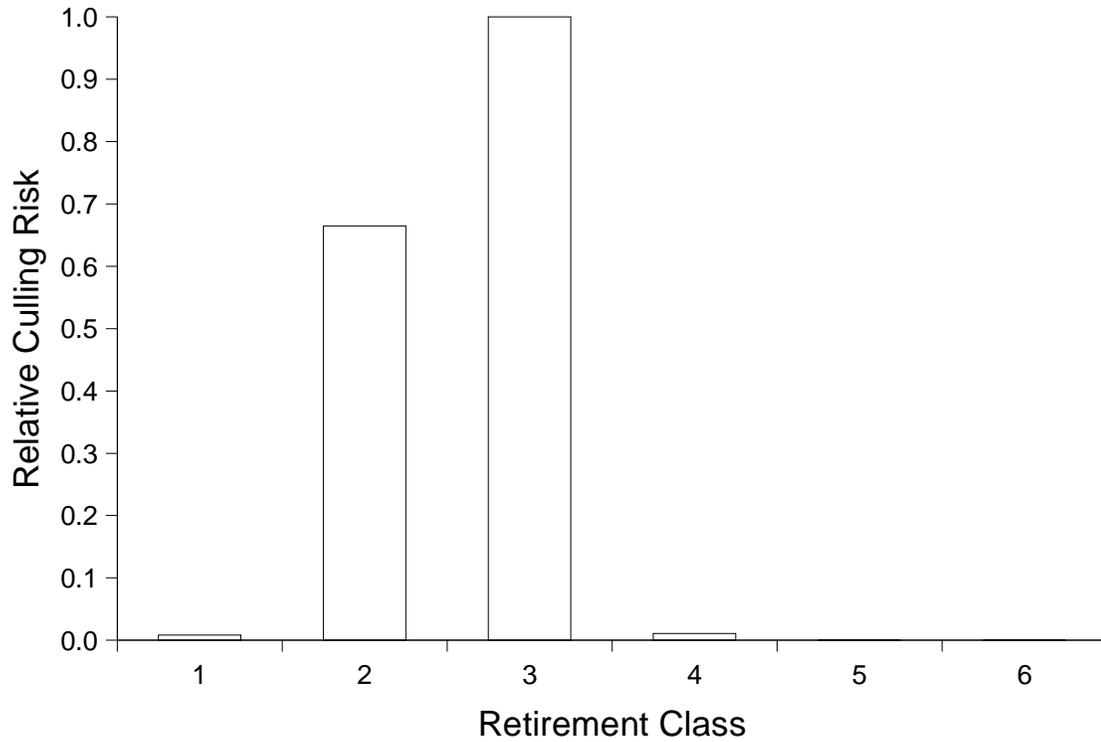


**Figure 4.8.** Estimates of the birth year effect for Early Working Life in Labrador Retrievers.

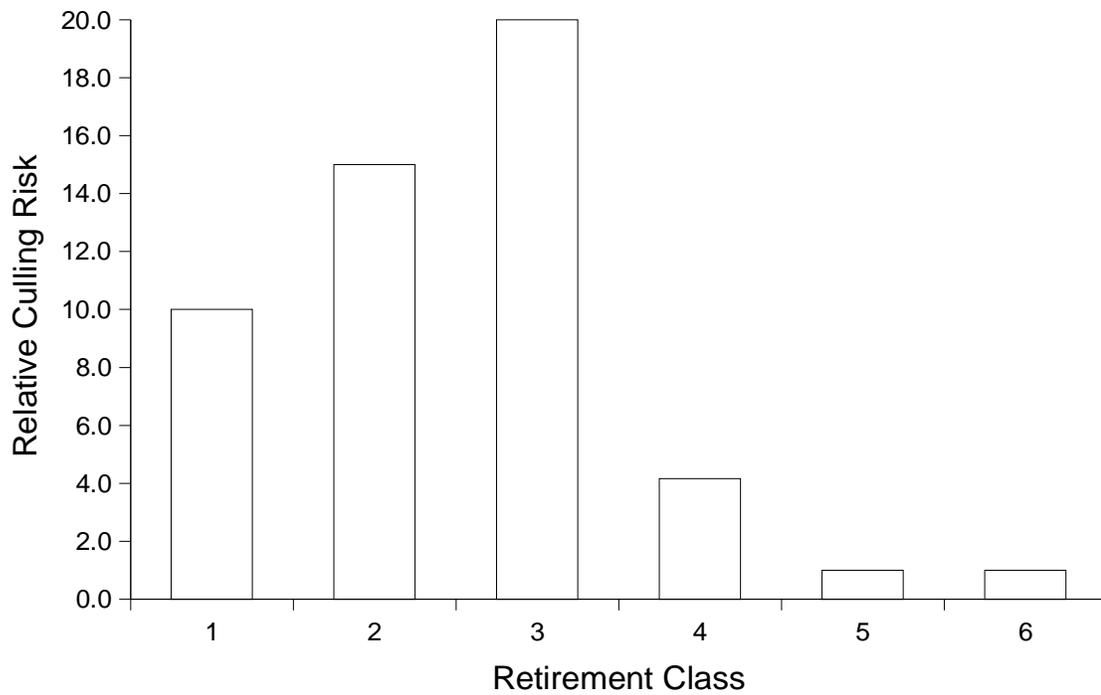
Litters born in a common year only shared a common environment until weaning. At weaning, puppies were distributed to puppy raisers, and litters were split up. Further, not all animals in a litter were selected for use as guides.

Figures 4.9 and 4.10 display relative culling risks for retirement classes in GS and LR, respectively. Labrador Retrievers were much more likely to be culled for health reasons, class 1, than GS. For both breeds, animals were more likely to be retired for temperament, class 3, than any other reason. Class 2 represents records for which no reason for retirement was given, and certainly contains records which properly belong in other classes. The Seeing Eye, Inc. does not use a standard set of codes representing culling reasons, and in some cases handlers never report reasons for the retirement of their guides. Risks of culling due to issues with the handler (class 4) or the dog currently being in service (class 6), were similar to the baseline. Class 5, lack of knowledge of the dog's current status, was the baseline risk. These results are consistent with expectations. Dogs usually retire from service as guides due to temperament or health reasons. In a small number of cases handlers suffer from age- or health-related disorders which reduce their mobility and results in the cessation of their use of their dogs as guides, although the dogs may still be quite valuable to their handlers as companions.

Figures 4.11 and 4.12 display relative culling risks for parity of dam in GS and LR, respectively. There is not a clear pattern for GS, although it appears that risk of culling increases with dam parity. There is a decrease in culling risk after first parity and continuing until parity 5 for LR. Dams retained for several



**Figure 4.9.** Estimates of the retirement class effect for Early Working Life in German Shepherds.

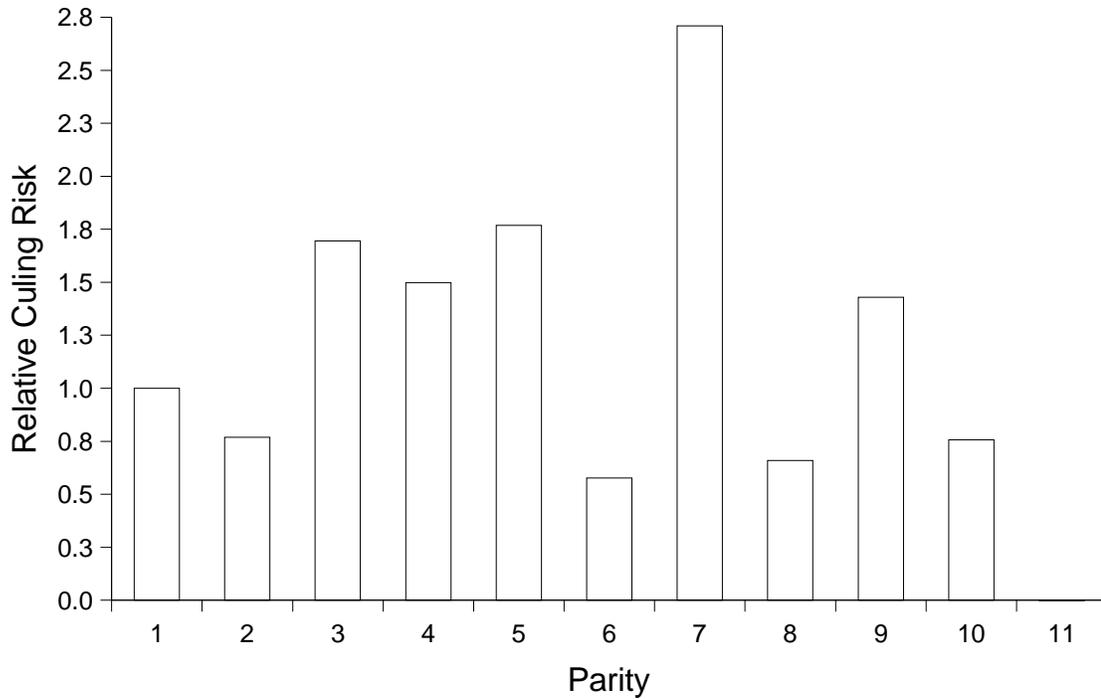


**Figure 4.10.** Estimates of the retirement class effect for Early Working Life in Labrador Retrievers.

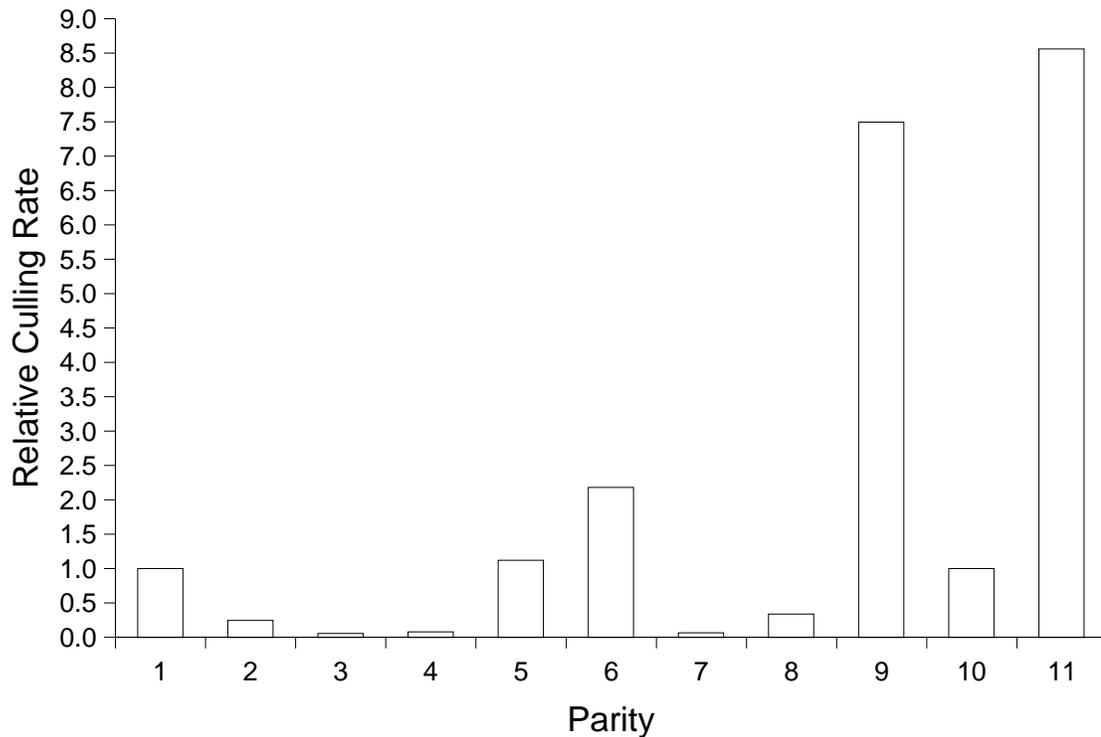
generations are probably superior animals which have produced high-quality litters, which is why there is not a consistently increasing risk with increasing parity.

Figures 4.13 and 4.14 display relative culling risks for handler age in GS and LR, respectively. The risk of culling is relatively constant over time for GS, with sharp increases in risk in middle age that decrease around [human] retirement age. There is a similar pattern in LR, although the increases in risk are in the 20-40 years of age group. Contrary to expectations, there is not a cumulative increase in risk with advancing age. It may be that increased risks of culling due to handler-related health problems associated with advancing age are offset by increased risks of culling due to poor dog health as a result of injury due to the greater mobility of younger dog guide users. There are peaks in risk in the early 60s, which corresponds to retirement age for most people. Presumably retirees decrease their use of guides when they no longer have jobs at which they must be present on a daily basis.

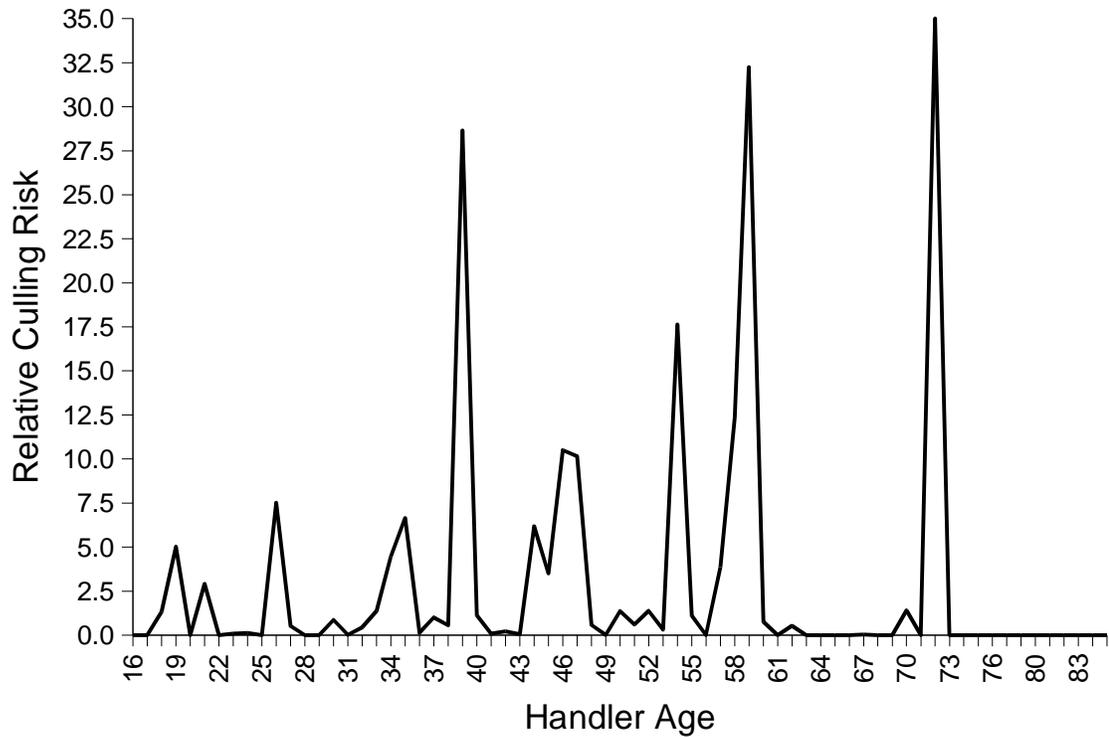
Female handlers of GS were 1.31 times as likely to have guides which retired than male handlers of GS. Female handlers of LR were 4.17 times as likely to be handlers of animals which were culled as male handlers of LR. Koda and Shimoju (1999) reported sex-of-human differences with respect to the initiation of contact between dogs and humans. It may be the case that women who use dog guides are less comfortable with their dogs than men who use guides. The difference in relative risk may also represent differences in socialization or rates of employment.



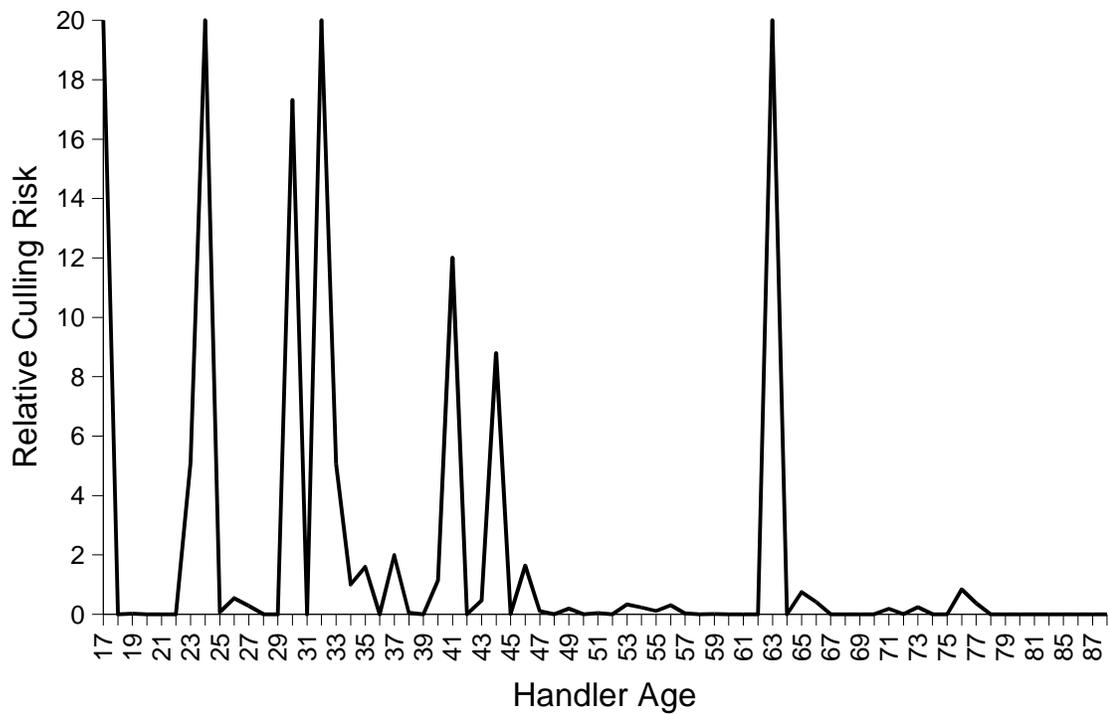
**Figure 4.11.** Estimates of the parity class effect for Early Working Life in German Shepherds.



**Figure 4.12.** Estimates of the parity class effect for Early Working Life in Labrador Retrievers.



**Figure 4.13.** Estimates of the handler age class effect for Early Working Life in German Shepherds.



**Figure 4.14.** Estimates of the handler age class effect for Early Working Life in Labrador Retrievers.

Inbreeding was identified as significant by the likelihood ratio test, but it is unclear how inbreeding influences working life. The estimate of the slope of the regression line,  $\beta_1$ , was  $-12.40 \pm 10.25$  for GS and  $-3.21 \pm 16.46$  for LR. The P-values for the test  $\beta_1 = 0$  were 0.226 and 0.846 for GS and LR, respectively. The estimates of  $\beta_1$  imply that increasing levels of inbreeding result in a loss of days of working life, or alternatively, result in an increased risk of culling. However, given the lack of statistical significance, it is unclear how these results should influence decision making.

### **Late Working Life**

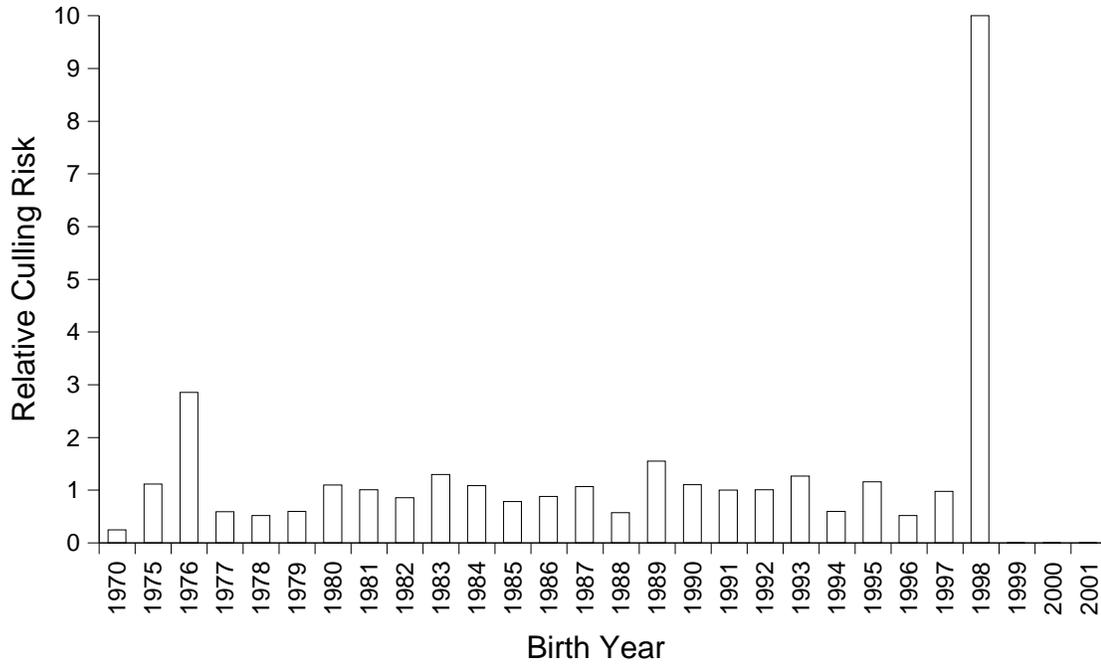
Female GS dog guides were as likely to retire as male GS, with a risk ratio of 1.01. The same relative risk was observed for LR, with females being slightly more likely to retire. While gender-of-animal is statistically significant in the model fit for LWL, the observed differences are of little practical significance. There is no reason to preferentially select one sex of dog guide over another for the purpose of maximizing working life.

Figures 4.15 and 4.16 display relative culling risks for birth year in GS and LR, respectively. For both breeds, the risk functions increase gradually over time. There is an increased risk of culling for GS in 1976, which corresponds with the previous period of rapid expansion discussed for EWL. The LR risk only increased above the reference point starting in 1992. The risks are very high at this point in time because all of the LR born in 1999 and 2001 are censored in the dataset; they have not yet worked long enough to have retired from service. In time, the risk function for 1999-2001 should decrease to one similar to that for

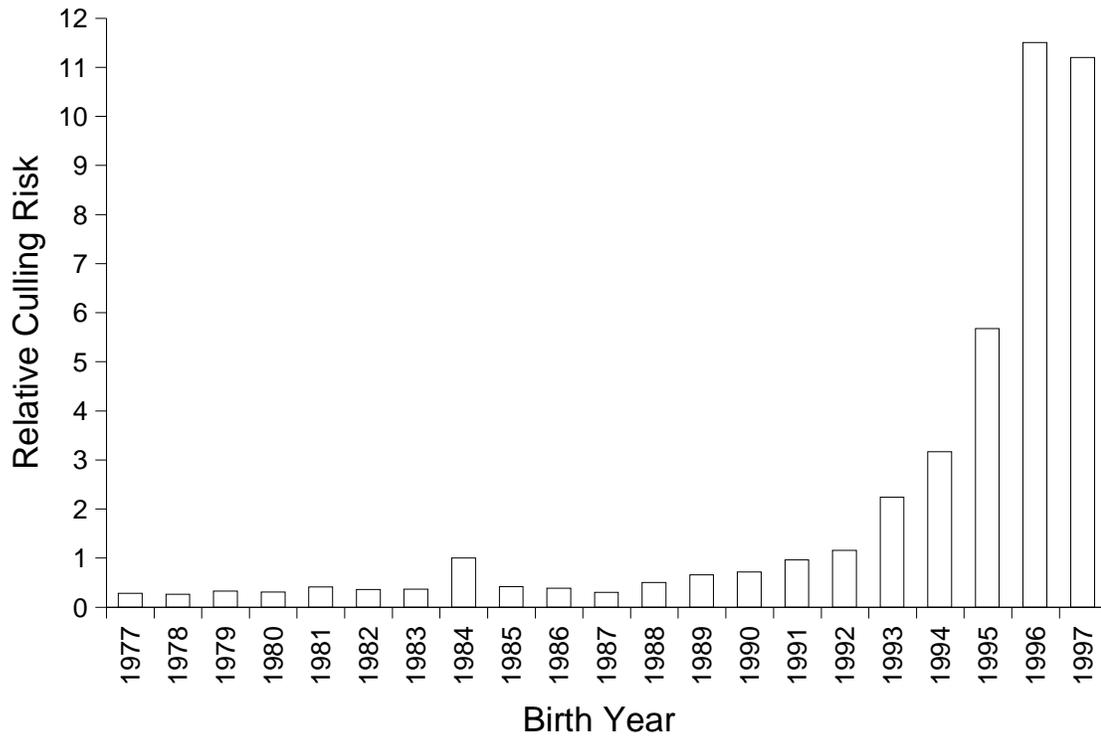
earlier years. The same situation has resulted in the very high relative risks for GS in the late 1990s.

There was a significant litter effect for GS and LR for LWL. A figure is not provided as its interpretation would not be informative or helpful. Clearly there are differences between litters with respect to risk of retirement, but the reason for those differences is not clear. Littermates only share a common environment until they are weaned and sent to puppy raisers. However, one of the principal items considered when evaluating a dog for use as a guide by The Seeing Eye is hip quality. Leighton (1997) reported heritabilities of 0.35 and 0.45 for subjective hip quality and distraction index, which are measures of hip quality. Given that littermates will have, on average, the same EBVs for hip quality, the litter effect may be due to selection for suitability for training as a dog guide, rather than for longevity of service as a dog guide.

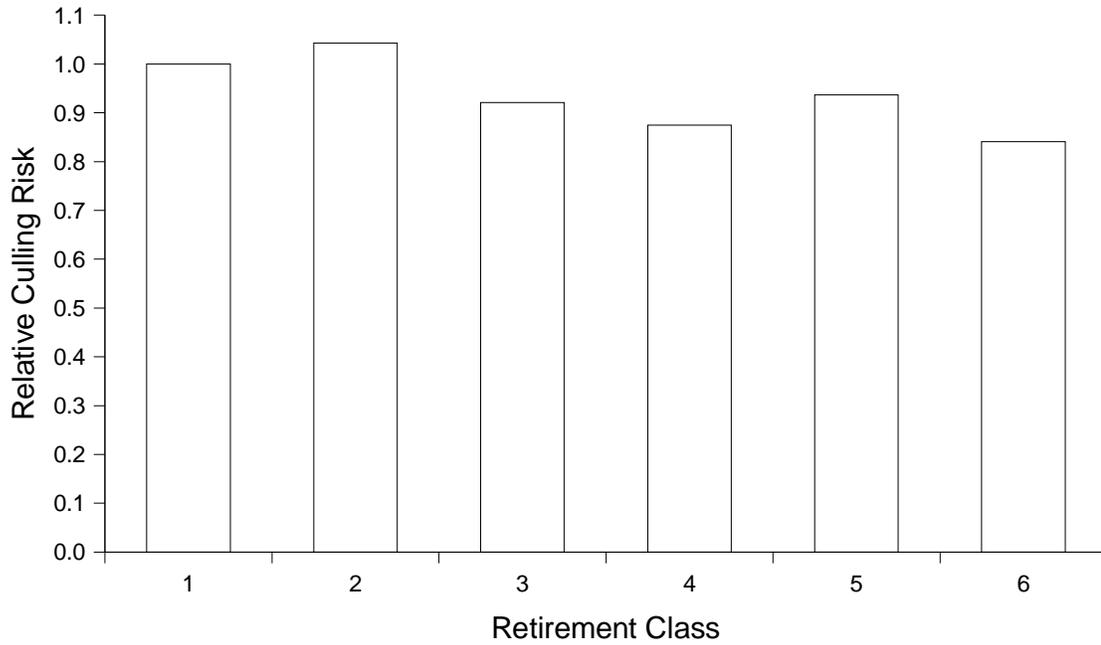
Figures 4.17 and 4.18 display relative culling risks for retirement class in GS and LR, respectively. There is very little variation in risk among the classes for GS. German Shepherds that have retired were slightly more likely to be in the retired, no comment group (class 2) than any of the others. The risk of retiring due to problems with temperament was slightly below average, which is contrary to the case for EWL. It appears that the behavioral problems that lead to retirement of GS guides are identified early in the working life of the animal. The LR risk profile for LWL is quite similar to that for EWL. Labrador Retrievers, however, were five times more likely to be culled for temperament than any other reason. These results imply that LR are retired for different behavioral problems



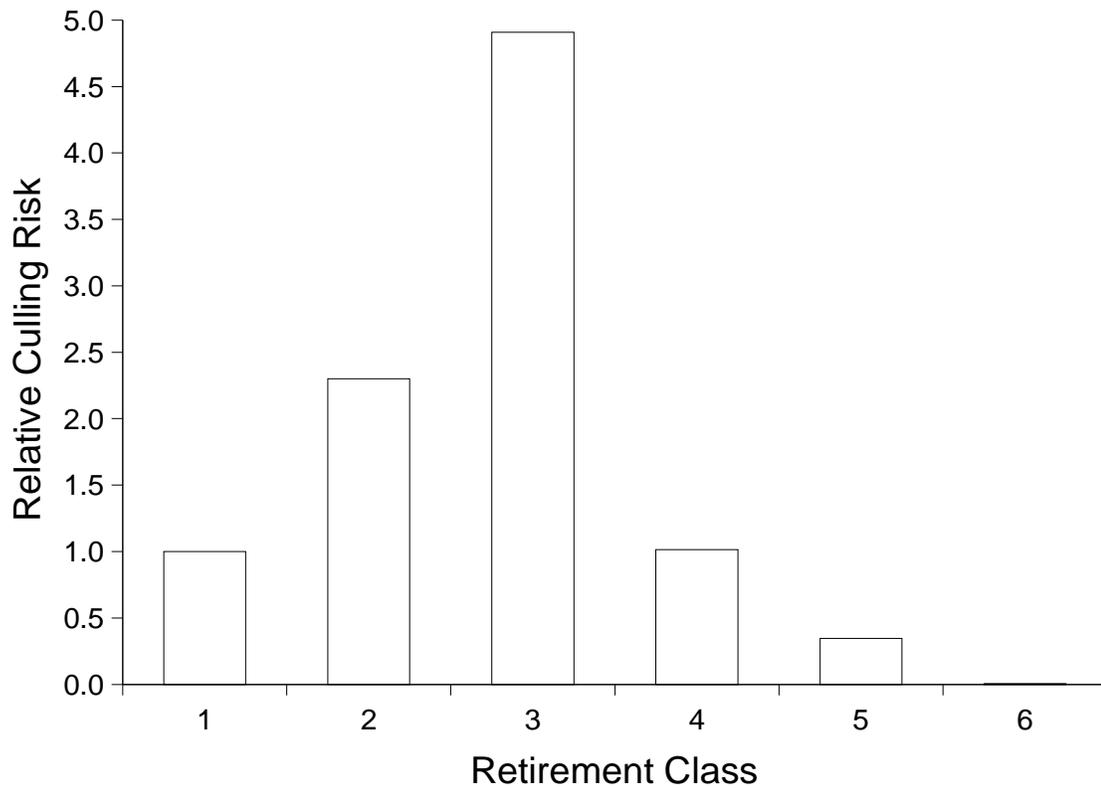
**Figure 4.15.** Estimates of the birth year class effect for Late Working Life in German Shepherds.



**Figure 4.16.** Estimates of the birth year class effect for Late Working Life in Labrador Retrievers.



**Figure 4.17.** Estimates of the retirement class effect for Late Working Life in German Shepherds.

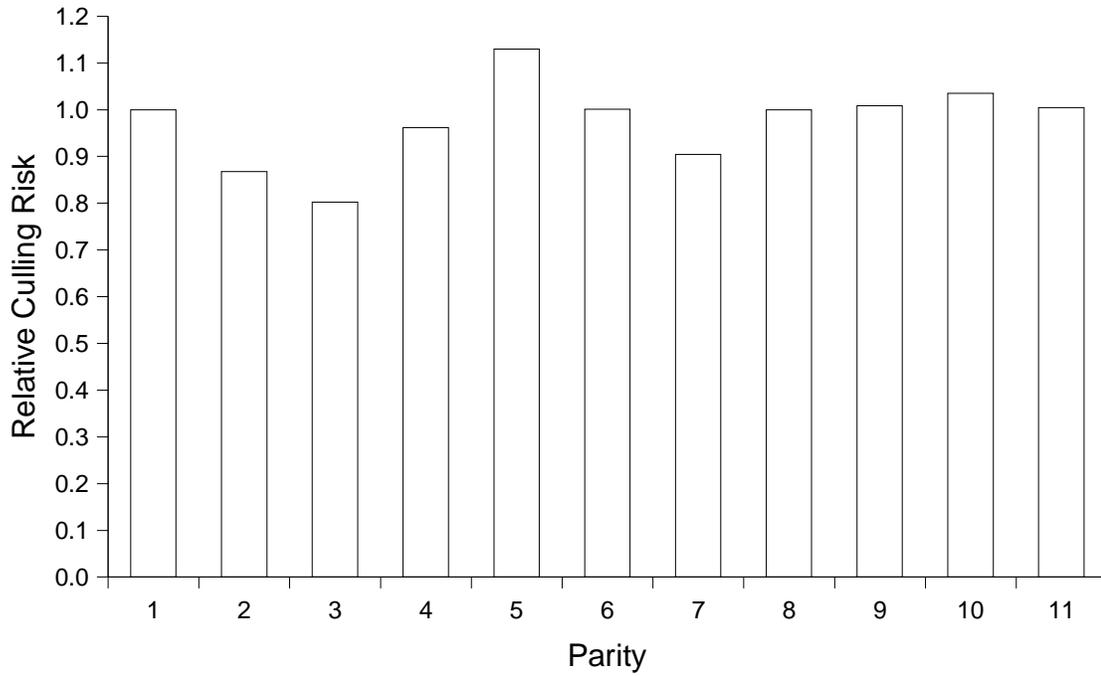


**Figure 4.18.** Estimates of the retirement class effect for Late Working Life in Labrador Retrievers.

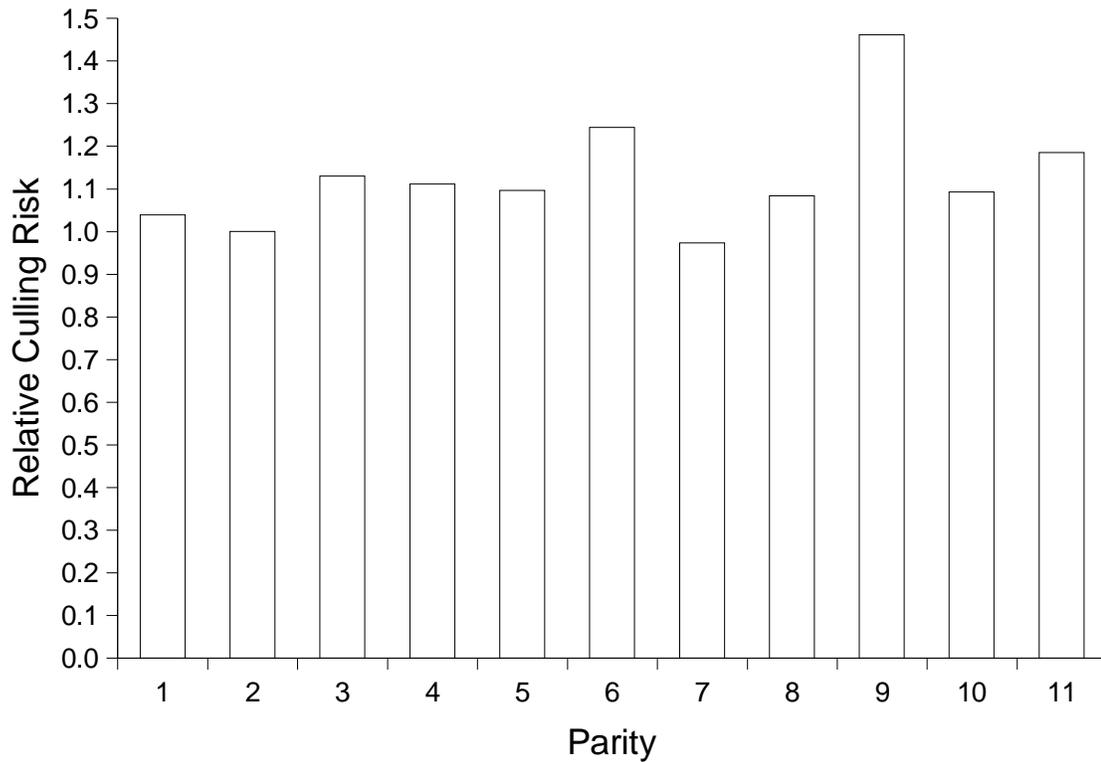
than GS, and that those problems are not necessarily identified early in a dog's working life.

Figures 4.19 and 4.20 display relative culling risks for parity in GS and LR, respectively. There is no suggestion that offspring of older GS dams are any more likely to be retired than offspring of young dams. There is a slight increasing risk in the LR with dam parity, but the magnitude of the change in risk is small. In some species, such as dairy cattle, it is reasonable to see an increase in culling risk with increasing parity. Given the high cost of producing dog guides, it is reasonable to produce multiple litters from the same dam once she has shown that her offspring have the mental and physical aptitude for guide work.

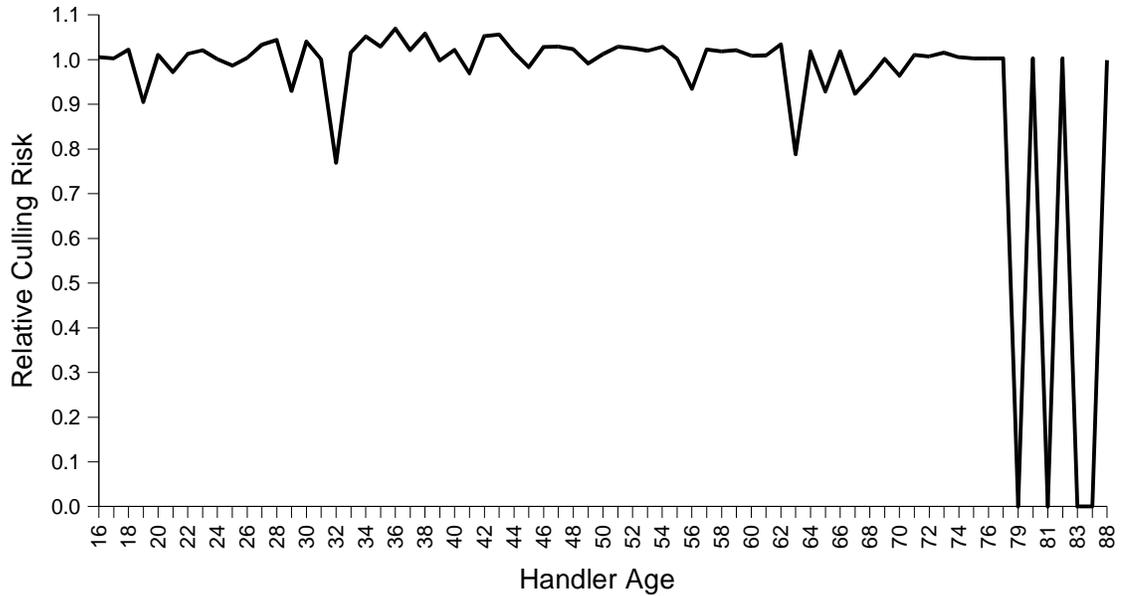
Figures 4.21 and 4.22 display relative culling risks for handler age in GS and LR, respectively. The risk function remains fairly constant with respect to handler age until about 80 in the GS and 70 in the LR. While there were characteristic increases in the risk function for EWL at around age 65, there were no such obvious peaks in the risk function for LWL, although there is an increase in risk for LR for handlers in their late fifties. There was a jump in risk for LR at age 70, which may correspond to the age at which many elderly individuals move into assisted living communities. Conclusions should be drawn about older handler ages carefully, however; for LR, there were less than 10 handlers in each age class starting at age 72, and in most cases there was only one handler that old. There may be a trend here that is not shown in the figures. Once a handler has had a dog for at least 18 months, they may be reluctant to return the dog



**Figure 4.19.** Estimates of the parity class effect for Late Working Life in German Shepherds.



**Figure 4.20.** Estimates of the parity class effect for Late Working Life in Labrador Retrievers.



**Figure 4.21.** Estimates of the handler age class effect for Late Working Life in German Shepherds.



**Figure 4.22.** Estimates of the handler age class effect for Late Working Life in Labrador Retrievers.

even if they are no longer using the dog actively as a guide. If that is the case, it would bias the data in such a manner as to conceal the fact that dogs paired with older handlers cease working as guides.

Female handlers of GS were about as likely to have guides which retired as male handlers of GS, with a risk ratio of 1.02. The results were similar for LR handlers, with female handlers having guides which were culled 1.05 times as often as male handlers. Given the small magnitude of this difference, it is not clear why the effect of handler gender was significant in the model. Whatever the reason for the difference in relative risk between male and female handlers for EWL, it does not appear to influence LWL. Perhaps female handlers are more likely to return their guides than male handlers during the first 18 months of service and return to using a cane, but are no more likely than males to cease using a guide after they have passed into the LWL period.

Inbreeding was identified as significant by the likelihood ratio test, but it is unclear how inbreeding influences working life. The estimate of the slope of the regression line,  $\beta_1$ , was  $0.259 \pm 10.25$  for GS and  $-0.130 \pm 1.149$  for LR. The P-values for the test  $\beta_1 = 0$  were 0.980 and 0.910 for GS and LR, respectively.

#### Parameter Estimates

Estimates of baseline hazards ( $\rho$ ), sire additive genetic variance ( $\sigma_s^2$ ), birth year gamma parameters ( $\gamma_{BY}$ ) and  $\log(h^2_{\log})$  and linear ( $h^2$ ) scale heritabilities are presented in Tables 4.9–4.12 for EWL and LWL in GS and LR, respectively.

**Table 4.9.** Estimates of parameters for Early Working Life in German Shepherds.

<b>Effect</b>	<b>Parameter</b>	<b>Value</b>
Baseline Hazard	$\rho$	$2.8082 \pm 1.000$
Sire variance	$\sigma_s^2$	0.7448
Birthyear	$\gamma_{BY}$	5.2046
Heritability (log scale)	$h_{\log}^2$	0.9504
Heritability (linear scale)	$h^2$	0.0318

**Table 4.10.** Estimates of parameters for Late Working Life in German Shepherds.

<b>Effect</b>	<b>Parameter</b>	<b>Value</b>
Baseline Hazard	$\rho$	$3.1077 \pm 1.000$
Sire variance	$\sigma_s^2$	0.3483
Birthyear	$\gamma_{BY}$	6.1229
Heritability (log scale)	$h_{\log}^2$	0.5949
Heritability (linear scale)	$h^2$	0.0179

**Table 4.11.** Estimates of parameters for Early Working Life in Labrador Retrievers.

<b>Effect</b>	<b>Parameter</b>	<b>Value</b>
Baseline Hazard	$\rho$	2.0954 $\pm$ 0.2210
Sire variance	$\sigma_s^2$	0.7088
Birthyear	$\gamma_{BY}$	4.5269
Heritability (log scale)	$h^2_{\log}$	0.9258
Heritability (linear scale)	$h^2$	0.0450

**Table 4.12.** Estimates of parameters for Late Working Life in Labrador Retrievers.

<b>Effect</b>	<b>Parameter</b>	<b>Value</b>
Baseline Hazard	$\rho$	0.9764 $\pm$ 0.0261
Sire variance	$\sigma_s^2$	0.1052
Birthyear	$\gamma_{BY}$	4.8421
Heritability (log scale)	$h^2_{\log}$	0.2268
Heritability (linear scale)	$h^2$	0.0317

German Shepherds has  $\rho > 2$  for EWL and LWL, indicating that the risk of retirement increased with time in service. Labrador Retrievers had  $\rho > 2$  for EWL and  $\rho = 1$  for LWL. It is reasonable to expect that  $\rho > 1$  for both breeds in this population because the risk of a dog retiring increases with age. The longer a dog works as a guide the more likely they will become ill, succumb to age-related disorders, or become injured. Owners age with their dogs, and as a dog ages they are increasingly likely to be paired with an owner of decreased mobility, which could result in the end of a dogs working life.

Estimates of the sire component of additive genetic variance were obtained and used to calculate log-scale heritabilities of EWL and LWL. The method of Ducrocq and Casella (1996) was used to convert log-scale estimates of heritability to a linear scale. That method requires the estimation of a parameter,  $\gamma_{BY}$ , associated with a random herd-year or herd-year-season effect. No such effect was operative in this population; however, in order to facilitate interpretation, a loggamma birth year effect was fitted using The Survival Kit. The estimates of  $\gamma_{BY}$  for this population were much smaller than herd-year or herd-year-season parameters reported in the literature (Boettcher et al, 1999; Dürr et al., 1999) and may have biased the estimates of the linearized heritabilities. Linearized heritabilities should always be interpreted carefully, and that is of particular importance in this case.

The heritability of EWL was 0.0318 in GS and 0.0450 in LR, respectively; the heritability of LWL was 0.0179 for GS and 0.0317 for LR, respectively. Standard errors were not available for either  $h^2_{\log}$  or  $h^2$ . In both

breeds,  $h^2$  was greater for EWL than for LWL. Heritabilities were higher for both traits for LR than GS, although the magnitude of the difference is small. The magnitude of heritability for various measures of productive life is typically on the order of 0.03 to 0.09 (Boettcher et al, 1999; Dürr et al., 1999; Jairath et al., 1998). The estimates of heritability presented in Tables 4.9 though 4.12 are small but consistent with the literature.

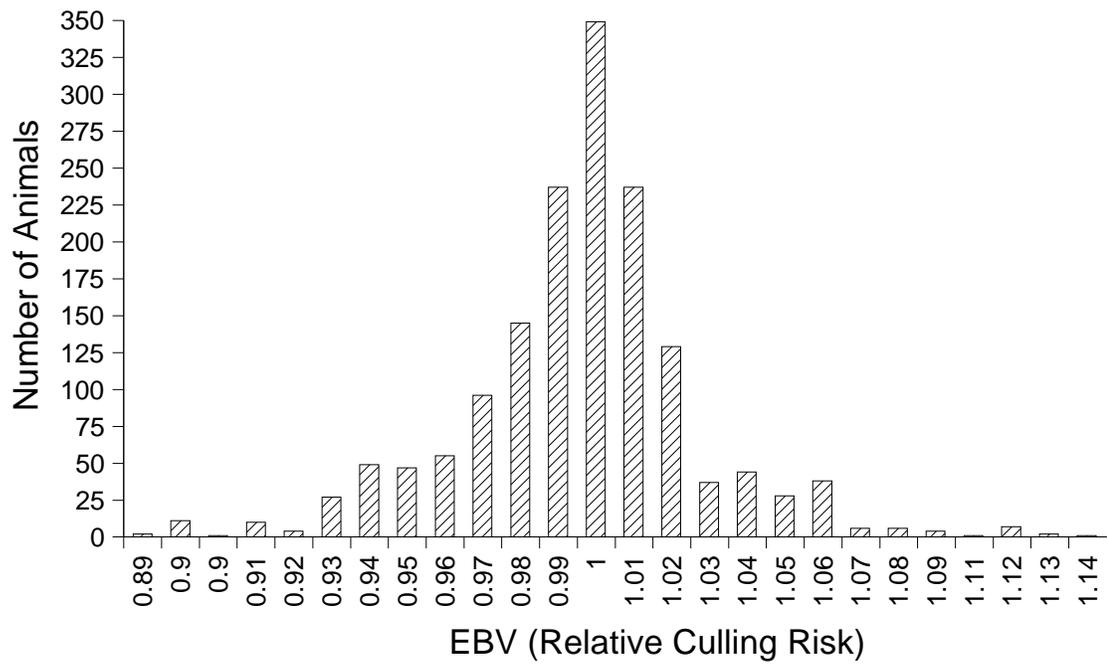
All attempts to estimate non-additive genetic effects by fitting a model with a loggamma full-sib effect failed to converge for either breed-trait combination, with  $\gamma$  going to  $+\infty$ . While there were many full-sib families produced by TSEI, only animals which worked as guides for blind people were included in this dataset. As a result, the actual number of full-sibs in the dataset was very small. It is unlikely that a reliable estimate of non-additive genetic variance can be obtained for this population unless a family selection scheme, which would increase the number of full-sibs trained and used as dog guides, is used to select animals for training in the future. Ducrocq et al. (2000) were able to estimate a full-sib effect from poultry data, but its magnitude was very small, 17% and 13% of the sire effect for early and later PL, respectively. Failure to account for a full-sib effect would result in small overestimation of  $\sigma^2_s$ , which would not change results significantly. There is no reason to suppose that there would be a significant non-additive effect for either working life trait in this population.

## Breeding Values

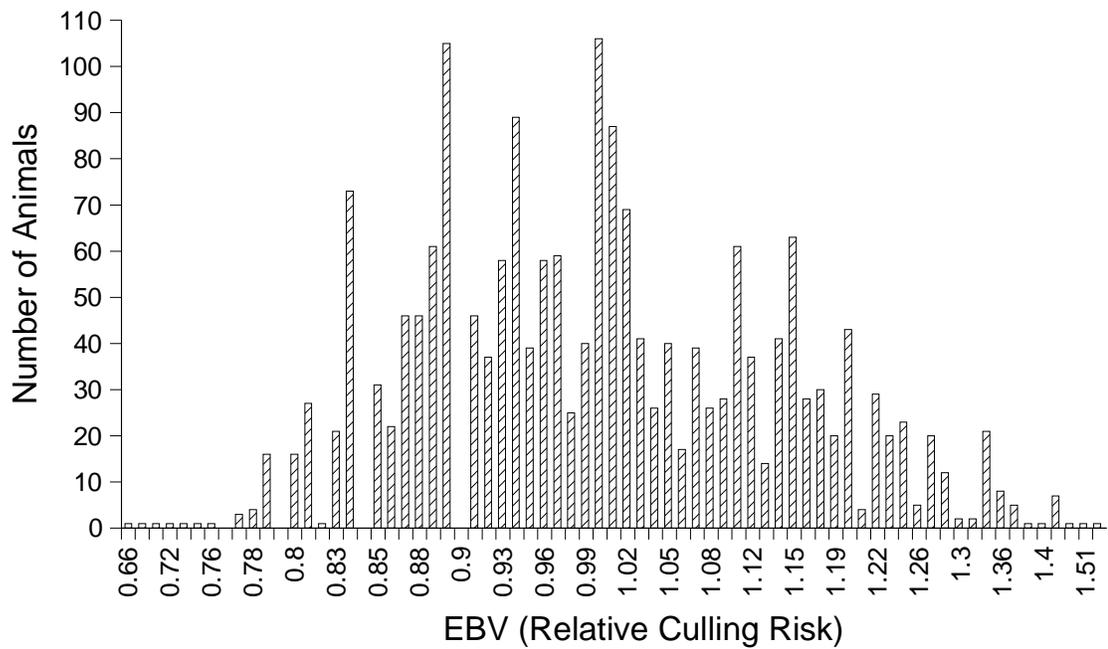
Sire EBVs are presented as relative culling risks, rather than days of working life, for ease of interpretation. Offspring of a sire with an EBV of 1.5 have a 50% greater chance, on average, of being culled than the offspring of an average sire (EBV=1.0).

Figures 4.23 and 4.24 represent sire EBVs for EWL in GS and LR, respectively. The distribution of GS EBVs is slightly left-skewed, while the distribution of LR EBVs is right-skewed. Estimated breeding values for LR have wider range than those for GS, which is consistent with the heritabilities reported above. Figures 4.25 and 4.26 represent sire EBVs for LWL in GS and LR, respectively. The distribution of GS LWL EBVs is more symmetric and much flatter than that for EWL. There are a large number of GS sires with EBVs close to 1.0, and those EBVs were rounded to 1.0 to construct Figure 4.25, emphasizing the concentration of EBVs around the mean. The LR EBVs possess a much more pronounced degree of left-skewness than for EWL. As for EWL, the distribution of EBVs is wider in LR than GS, reflecting the difference in the heritabilities of the two traits. It would be preferable to see left-skewed distributions of EBVs, which would correspond to reduced culling risks, than the right-skewed distributions in Figures 4.24 and 4.26. The short left tails are discouraging because they support the other data that there is very little genetic variation for reduced culling risk which can be utilized.

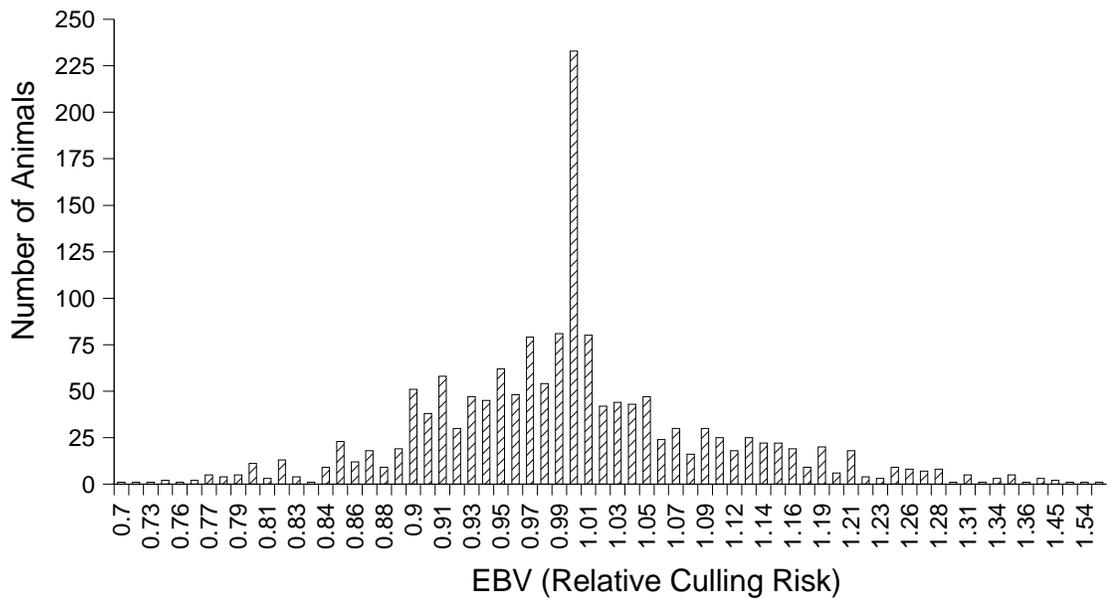
Genetic trend was estimated by regressing sire EBV on birth year. For both breeds regression coefficients (Table 4.13) were small, indicating that



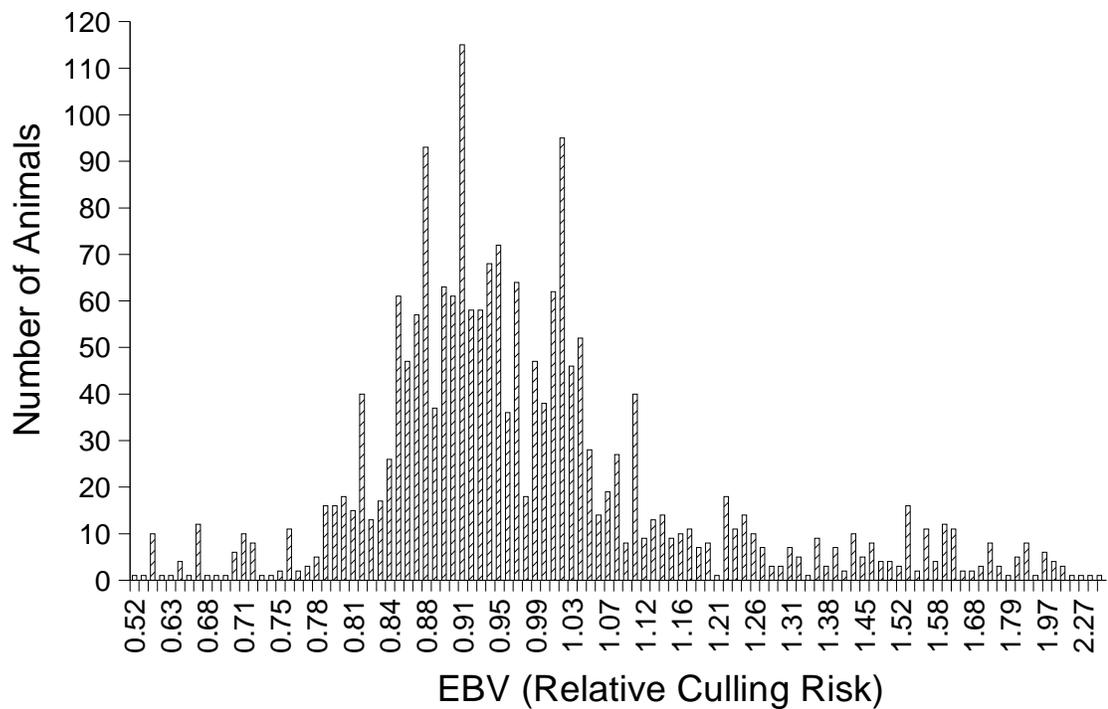
**Figure 4.23.** Estimated breeding values for Early Working Life in German Shepherds.



**Figure 4.24.** Estimated breeding values for Early Working Life in Labrador Retrievers.



**Figure 4.25.** Estimated breeding values for Late Working Life in German Shepherds.



**Figure 4.26.** Estimated breeding values for Late Working Life in Labrador Retrievers.

little change in EBVs for EWL has occurred. This is not surprising given the paucity of additive genetic variation in the trait. Genetic trend for LWL was similar to that for EWL (Tables 4.14). Regression coefficients for both traits in LR were much larger than those for GS, but the trend was small.

Pearson product-moment correlations and rank correlations between sire EBVs for EWL and LWL were small, negative, and not significantly different from zero ( $P < 0.05$ ) for each breed (Table 4.15). This was contrary to initial expectations, which suggested a moderate, positive correlation.

**Table 4.13.** Regression estimates of genetic trend for Early Working Life<sup>1</sup>.

<b>Breed</b>	<b>df<sup>a</sup></b>	<b>b<sub>0</sub><sup>b</sup></b>	<b>b<sub>13</sub><sup>c</sup></b>	<b>R<sup>2,d</sup></b>
GS	22	-2.6090	0.0007	0.0093
LR	24	52.4485	-0.0260	0.0528

<sup>1</sup>EBVs were regressed on four-digit year of birth (e.g. 1990).

<sup>a</sup>df = degrees of freedom.

<sup>b</sup>b<sub>0</sub> = y-intercept.

<sup>c</sup>b<sub>1</sub> = linear regression coefficient.

<sup>d</sup>R<sup>2</sup> = coefficient of determination

**Table 4.14.** Regression estimates of genetic trend for Late Working Life<sup>1</sup>.

<b>Breed</b>	<b>df<sup>a</sup></b>	<b>b<sub>0</sub><sup>b</sup></b>	<b>b<sub>1</sub><sup>c</sup></b>	<b>R<sup>2,d</sup></b>
GS	22	-2.6629	0.0019	0.0030
LR	24	-16.4322	0.0088	0.0316

<sup>1</sup>EBVs were regressed on four-digit year of birth (e.g. 1990).

<sup>a</sup>df = degrees of freedom.

<sup>b</sup>b<sub>0</sub> = y-intercept.

<sup>c</sup>b<sub>1</sub> = linear regression coefficient.

<sup>d</sup>R<sup>2</sup> = coefficient of determination

**Table 4.15.** Pearson and rank correlations between Early Working Life and Late WorkingLife estimated breeding values.

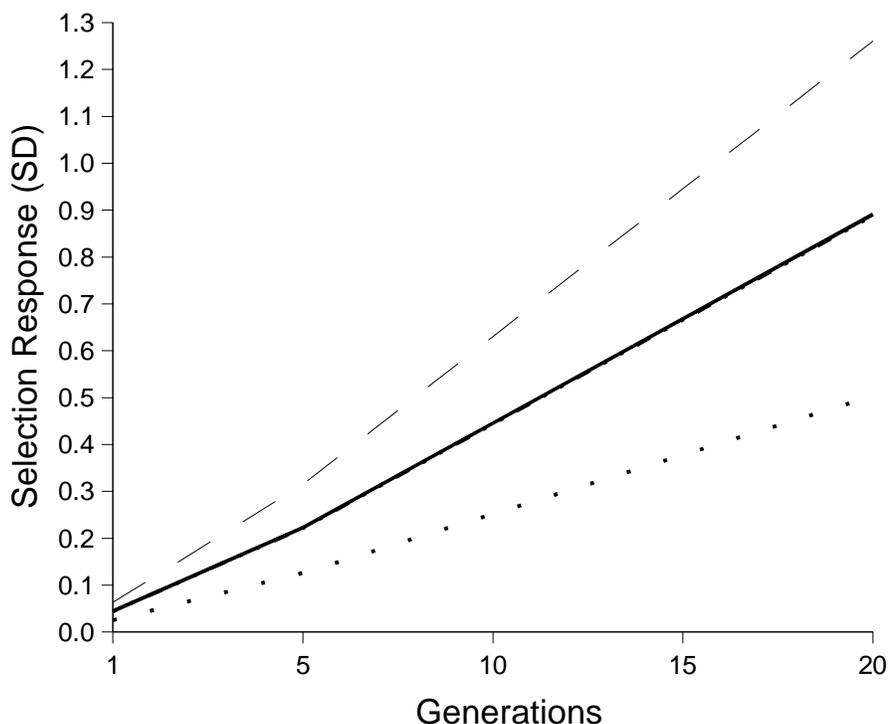
<b>Breed</b>	<b>Pearson Correlation</b>	<b>Rank Correlation</b>
GS	-0.07	-0.06
LR	-0.04	-0.01

## CHAPTER 5

### SUMMARY AND IMPLICATIONS

A population of GS and LR dog guides was analyzed to assess the allelic diversity and measure the amount of genetic variation for working life in the population. The population has been subjected to selection for hip quality and aptitude as a guide using BLUP breeding values for several generations. Breeding stock are chosen from the population of guides produced, with occasional importation of individuals from outside of the colony. All replacements are produced by the breeding colony.

Before recommendations can be made as to the optimal breeding scheme for a population, estimates of genetic parameters must be obtained. The results in this case are rather disappointing. The heritability of working life in both breeds of dog guide is very small, and ranges from 0.018 for LWL in German Shepherds to 0.045 for EWL in Labrador Retrievers. Assuming a phenotypic standard deviation of 1, a selection intensity of 1.4 (corresponding to the top 20% of individuals in the population each generation), and the heritabilities presented in Tables 4.1-4.4, an estimate of selection progress for each trait can be produced (Figure 5.1) (Cameron, 1997). Note that this figure assumes that working life is the only trait under selection. The best-case results indicate that more than 20 generations of breeding would be required. With a 24-month generation interval (Chapter 2), that would correspond to selecting for a single objective for 40 years. Clearly this is an unreasonable objective. In such cases, the typical approach would be to construct a selection index with a set of



**Figure 5.1.** Theoretical response to selection for German Shepherd Early Working Life (bold line), Labrador Retriever Early Working Life (solid line), German Shepherd Late Working Life (dotted line), and Labrador Retriever Late Working Life (broken line) (SD=1;  $i=1.4$ )

weights which reflects the economic values of the traits of interest. The phenotypic and genetic correlations between EWL, LWL, and other traits of interest, such as subjective hip quality or distraction index, required to construct a selection index are not yet available.

The estimates of genetic trend reported in Chapter 4, however, suggest that there is no need for concern about selection pressure against longevity. Indeed, there is reason to suspect that a great deal of indirect pressure is exerted on EWL, LWL, and other traits affecting longevity. Dogs selected for use as guides have passed a rigorous series of health and aptitude

exams, which would select for EWL in particular. The use of dogs which have already worked for some time as guides would have the benefit of applying selection pressure in favor of LWL. In fact, while many breeding schemes favor reproduction at the earliest possible age in order to reduce generation intervals, such schemes are contraindicated in the case of dog guides. Smart animals with good temperament, high-quality hips, and a genetic predisposition towards long working lives are much more desirable than animals produced in as short a time interval as possible. In addition, the time required for rearing, screening, and training dog guides would not be significantly reduced by shortening generation intervals by three or four months.

The results with respect to genetic diversity are more promising than the levels of inbreeding and relationship in the population might suggest. Effective founder and ancestor numbers have been slowly increasing over time, and there is a clear trend towards increased heterozygosity in the number of founder genome equivalents in the population. Steps taken in the past few years to limit the number of matings for sires and dams has led to a plateau for inbreeding and relationship levels, and will no doubt result in a slight decline in those levels over time.

The importation of breeding stock from outside of the colony should be considered carefully. Animals provided by commercial breeders are only desirable in that they are not closely related to any animals currently in the breeding population. However, given the poor quality genetics for hips, eyes, and temperament in many families, commercial breeders are not a suitable

source of new breeding stock. The Seeing Eye, Inc. should look to other dog guide schools in the United States or abroad. Guide Dogs for the Blind, Inc. in California or the Guide Dogs for the Blind Association of Great Britain are attractive candidates for such an exchange, although any producer of dog guides which has a staff or consulting geneticist should be considered. Less attractive, but more numerous, are the many organizations which produce service animals for persons with disabilities. Ultimately it is important that any partner have high-quality animals and good records on those animals.

The exchange of germplasm between guide organizations would only serve to improve the genetic quality of all participating organizations, but there are some points to consider. First, while all programs have probably selected for similar traits, the traits measured may not be identical. Research would be required to determine how to combine all of the available information for genetic evaluation. The work of the Interbull group in the dairy world would provide a starting point for that work. The temptation to overuse outside breeders must also be overcome. Each population is a homogeneous island from a genetic point of view, and the exchange of animals among those islands will ultimately result in the homogenization of those populations. When populations are intermingling, the overuse of outstanding individuals results in a loss of genetic variability from the entire population which uses the same pool of parents. When there are distinct islands in the population, an island which has become too homogeneous can import new animals. A population which has lost more heterozygosity than is desired has no place to turn for new alleles. In the case of

dog guide breeders, a depletion of genetic variability would necessitate the use of commercially available breeding stock, which would have the net effect of reducing selection pressure for the traits of interest in the population. This sort of problem has become an issue of great concern to dairy cattle breeders, as 25% of the genes in the Holstein-Friesian breed may be traced back to a single individual.

The use of crossbred animals is not practical in some livestock species due to the economics of production, but there are no such constraints on dog guides. The data needed to assess the magnitude of heterotic effects for longevity are currently unavailable, but there is no reason to suppose that there would be a negative effect. While hips are not a problem with dog guides at the moment, there are concerns about progressive retinal atrophy; other genetic disorders may be of concern in the future. The use of crossbred animals is a good way to avoid combining deleterious alleles for inherited disorders.

Temperament is something of a problem in German Shepherds, so a cross of German Shepherds with Labrador Retrievers might result in animals with more suitable temperaments. There is another advantage to using crosses to produce guides: it removes any short-term need for new breeding stock in the colony.

The early generations of crossbred animals would have low levels of inbreeding and relationship and high effective founder numbers, effective ancestor numbers, and founder genome equivalents. Should it not prove possible to exchange breeding animals with other producers of dog guides, a pilot crossbreeding

program should be established. The Seeing Eye, Inc. has already begun to produce a small number of crossbred animals.

There is another alternative to germplasm exchange and crossbreeding which has not yet been discussed: the use of nontraditional breeds as guides. This idea may initially seem attractive, and indeed breeds such as the Beagle have been successfully employed as assistive animals for persons with disabilities for some years. However, animals used as dog guides must meet a stringent set of criteria. The dogs must be large enough to guide their handler by interacting with them physically; they must be highly intelligent and possess superior situational awareness; they must possess an outstanding temperament due to their interactions with people and other animals in stressful situations; and they must be superbly healthy. The required stature alone imposes a substantial limitation on the breeds from which guides may be selected. Any program embarking upon the use of a nontraditional breed would also be discarding years, and in some cases decades, of breeding for suitability to guide work. Seedstock would have to be obtained from commercial breeders, and the number of animals evaluated to obtain a guide would probably be much higher than for German Shepherds or Labrador Retrievers. Therefore, nontraditional breeds are not an appealing option for current producers of dog guides.

Selection of sires and dams on BLUP breeding values for hip quality and aptitude should continue. Constraints should be placed on matings with respect to future expected inbreeding or some measure of kinship, such as the K

value used by the American Jersey Cattle Club for their young sires. An exchange of breeding animals between dog guide schools should take place. Pilot crossbreeding programs should be implemented by one or more dog guide producers to determine the suitability of crosses for use as dog guides. Producers of dog guides which do not work with a geneticist in either a staff or a consulting role should enter into such an arrangement to insure the long-term health and viability of their population.

Selection of dog guides on an index of hip quality and aptitude as a guide has not resulted in longer working lives. The genetic trend for both EWL and LWL over more than twenty years has been zero. Aptitude and temperament should be reviewed to determine if there is an antagonistic relationship between the two traits. Dog guides were much more likely to retire due to temperament than any other reason in the first 18 months of service, suggesting that aptitude for guide work is correlated with other less desirable behaviors. As a result, selection for aptitude will result in increased relative culling risks for temperament and reduced genetic variation for EWL. The use of alternative tools for parent selection, such as pedigree analysis, may be more effective than direct selection for hip quality and aptitude.

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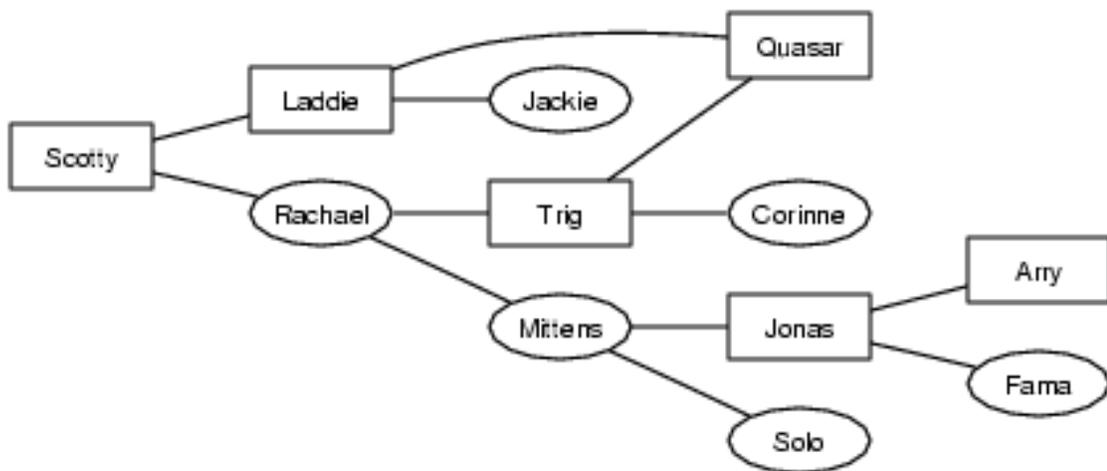
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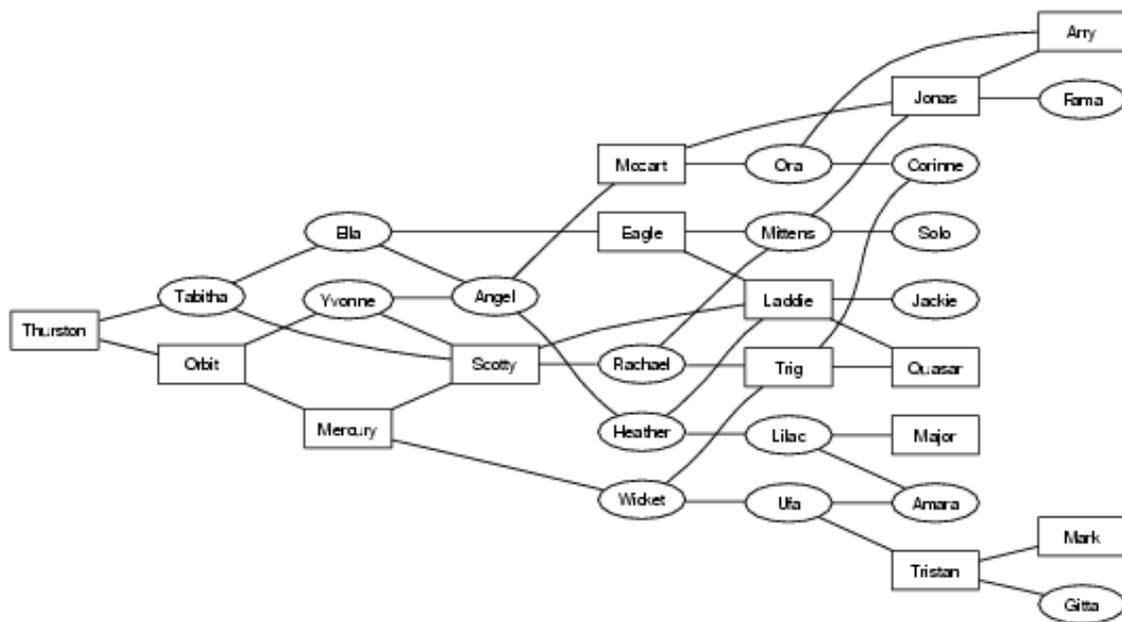
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## **APPENDIX 1**

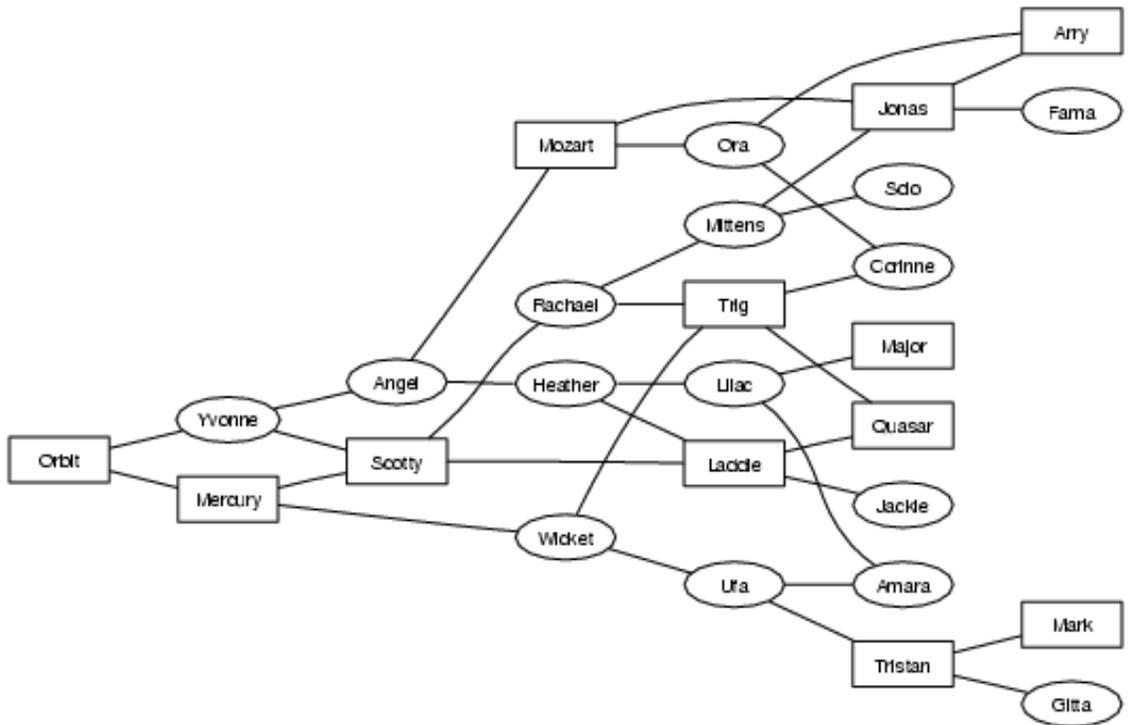
### **PEDIGREES OF THE TEN GERMAN SHEPHERD SIRE WITH THE HIGHEST AVERAGE COEFFICIENT OF RELATIONSHIP TO THE BREED**



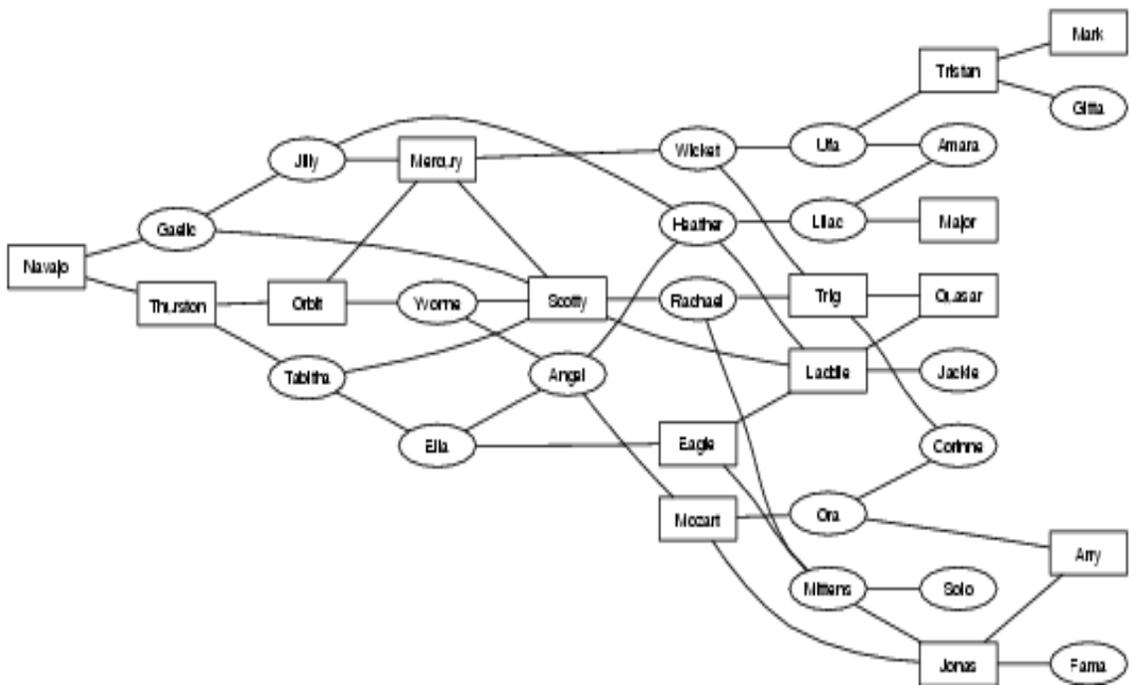
Appendix Figure 1.1. Scotty ( $r_{\text{breed}} = 0.305$ ;  $f = 0.063$ )



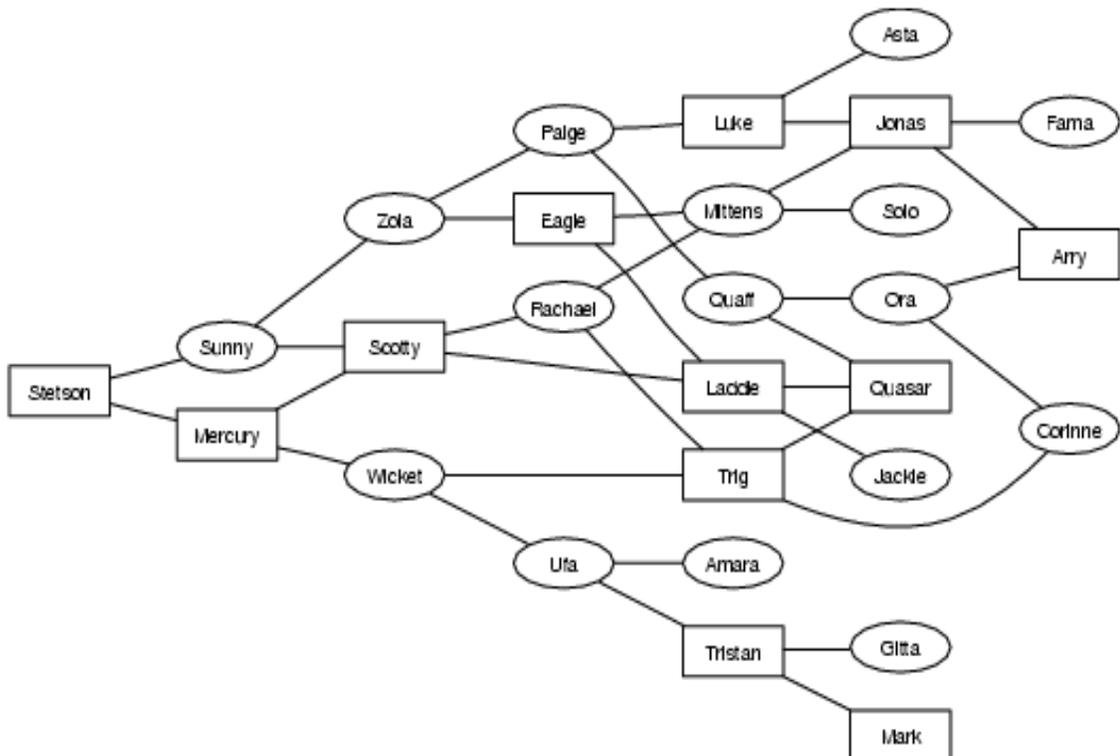
Appendix Figure 1.2. Thurston ( $r_{\text{breed}} = 0.277$ ;  $f = 0.237$ )



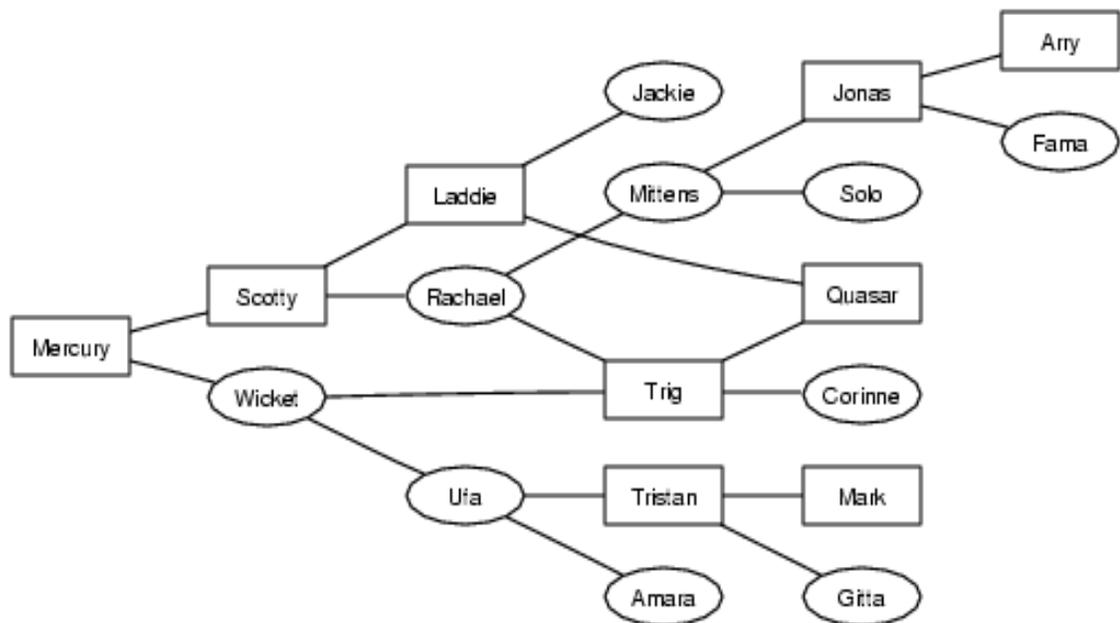
Appendix Figure 1.3. Orbit ( $r_{\text{breed}} = 0.275$ ;  $f = 0.192$ )



Appendix Figure 1.4. Navajo ( $r_{\text{breed}} = 0.275$ ;  $f = 0.274$ )

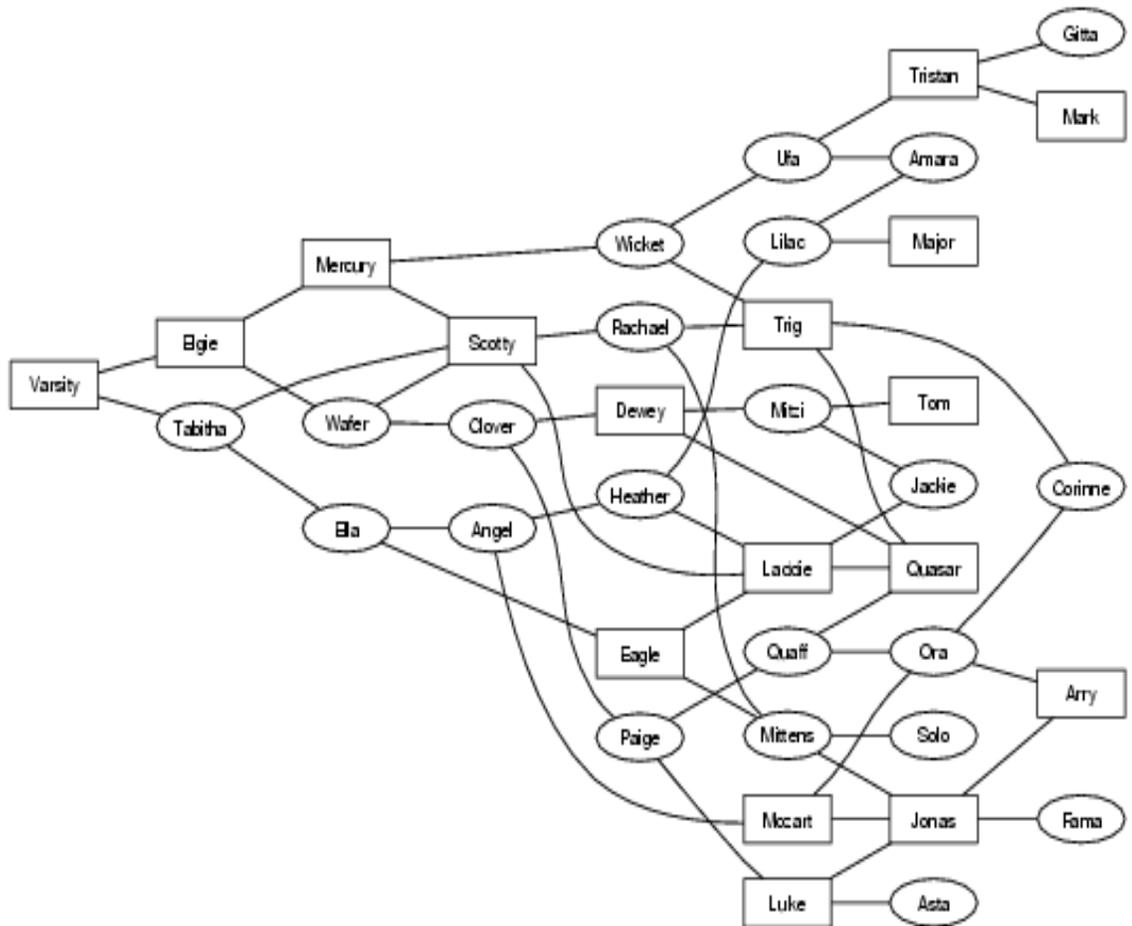


Appendix Figure 1.5. Stetson ( $r_{\text{breed}} = 0.273$ ;  $f = 0.201$ )

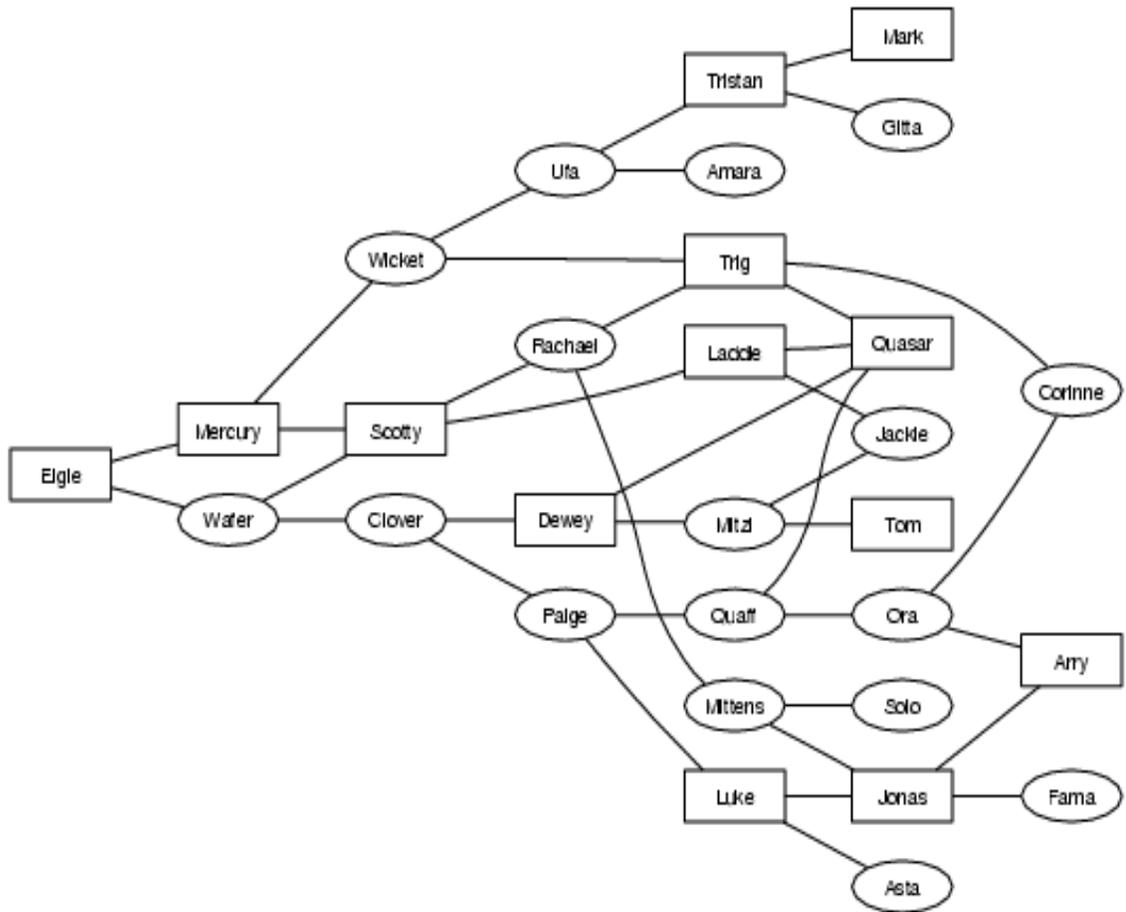


Appendix Figure 1.6. Mercury ( $r_{\text{breed}} = 0.272$ ;  $f = 0.094$ )





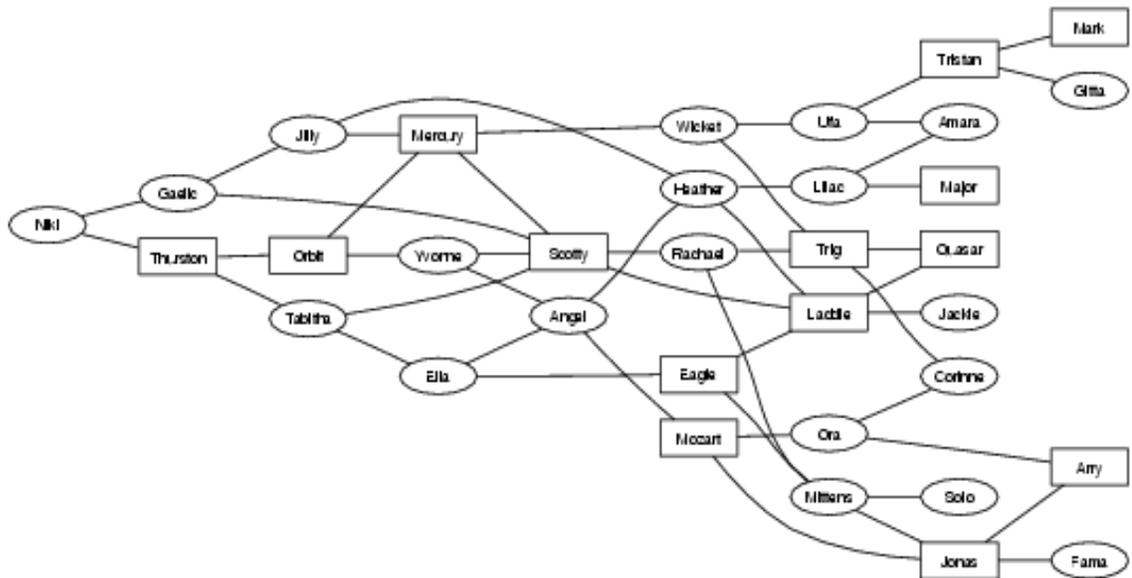
Appendix Figure 1.9. Varsity ( $r_{\text{breed}} = 0.267$ ;  $f = 0.209$ )



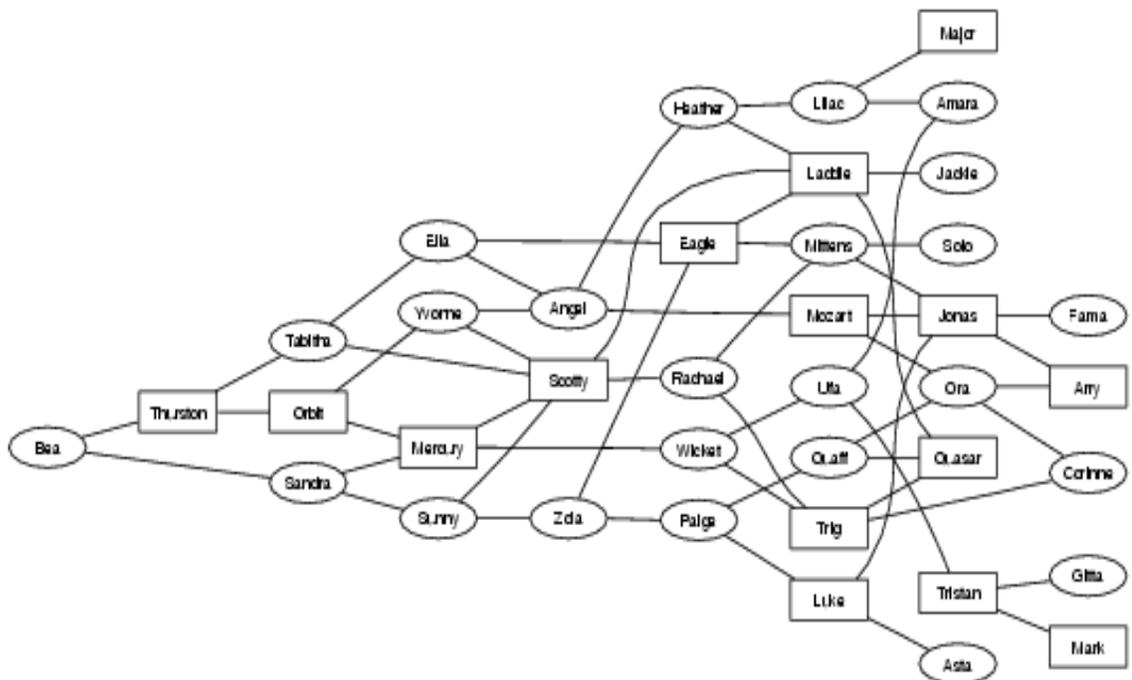
**Appendix Figure 1.10.** Elgie ( $r_{\text{breed}} = 0.264$ ;  $f = 0.195$ )

## **APPENDIX 2**

### **PEDIGREES OF THE TEN GERMAN SHEPHERD DAMS WITH THE HIGHEST AVERAGE COEFFICIENT OF RELATIONSHIP TO THE BREED**

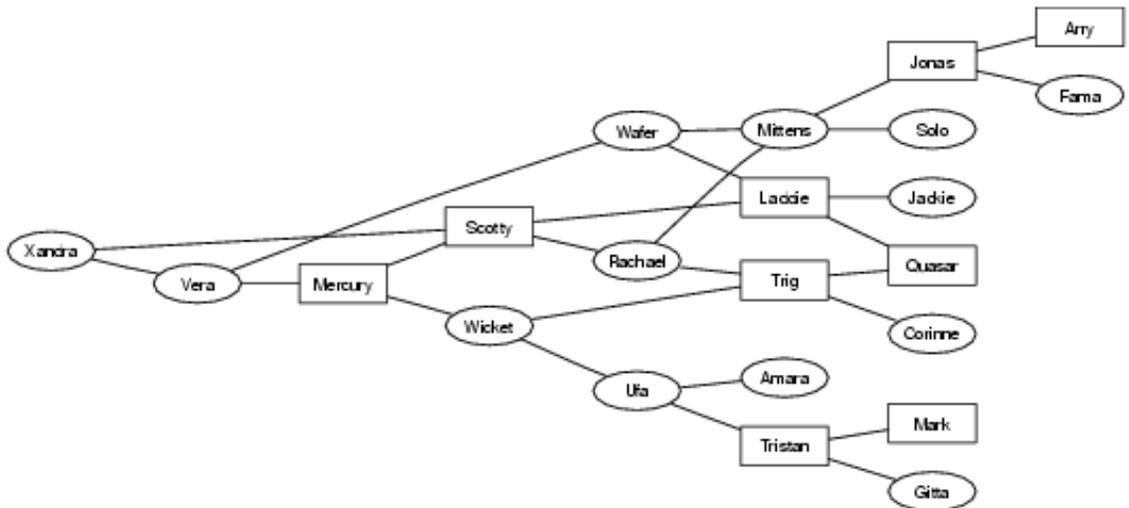


Appendix Figure 2.1. Niki ( $r_{\text{breed}} = 0.273$ ;  $f = 0.274$ )

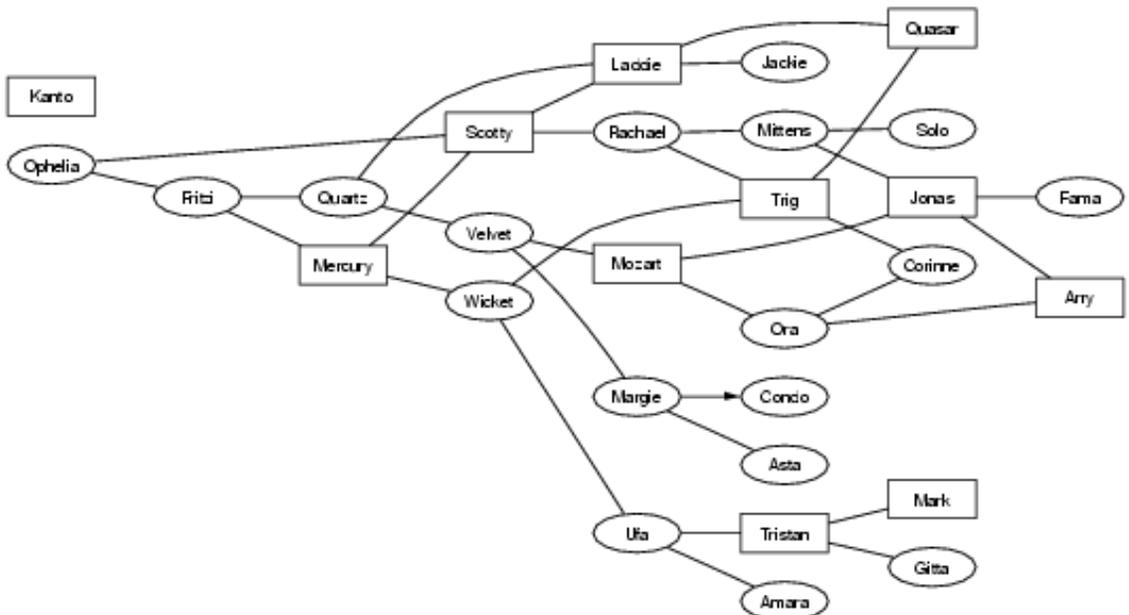


Appendix Figure 2.2. Bea ( $r_{\text{breed}} = 0.272$ ;  $f = 0.259$ )



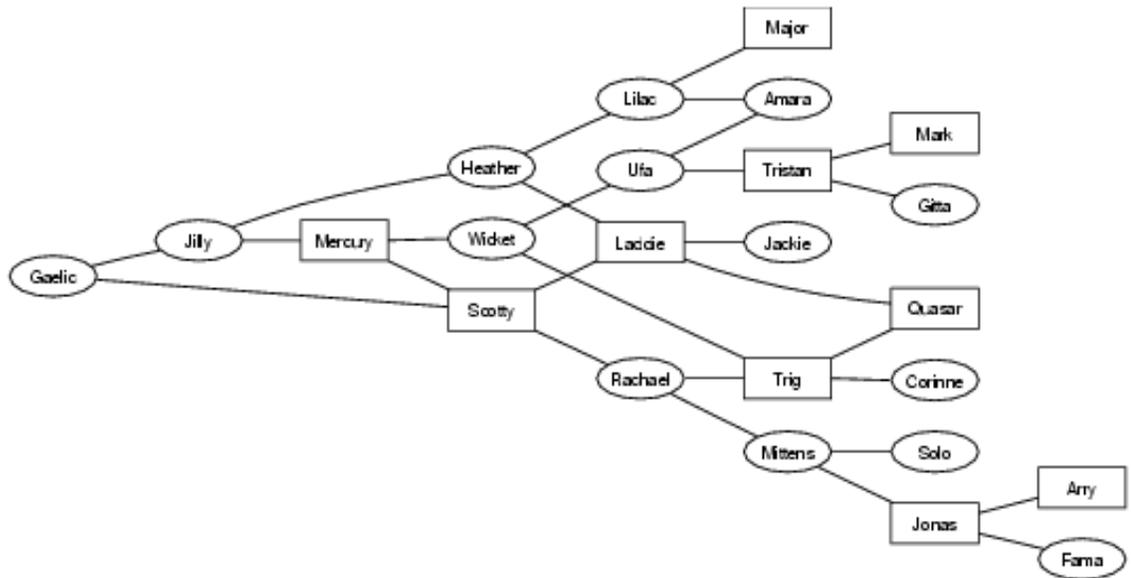


Appendix Figure 2.5. Xandra ( $r_{\text{breed}} = 0.269$ ;  $f = 0.258$ )

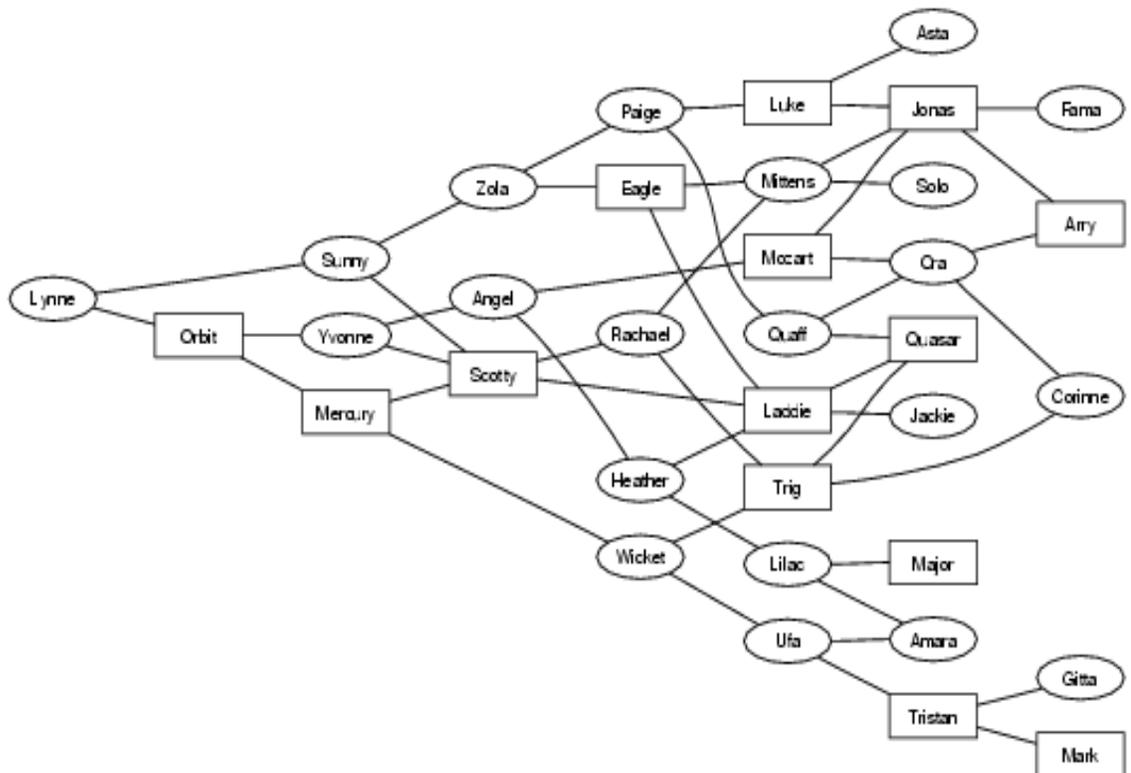


Appendix Figure 2.6. Ophelia ( $r_{\text{breed}} = 0.269$ ;  $f = 0.233$ )





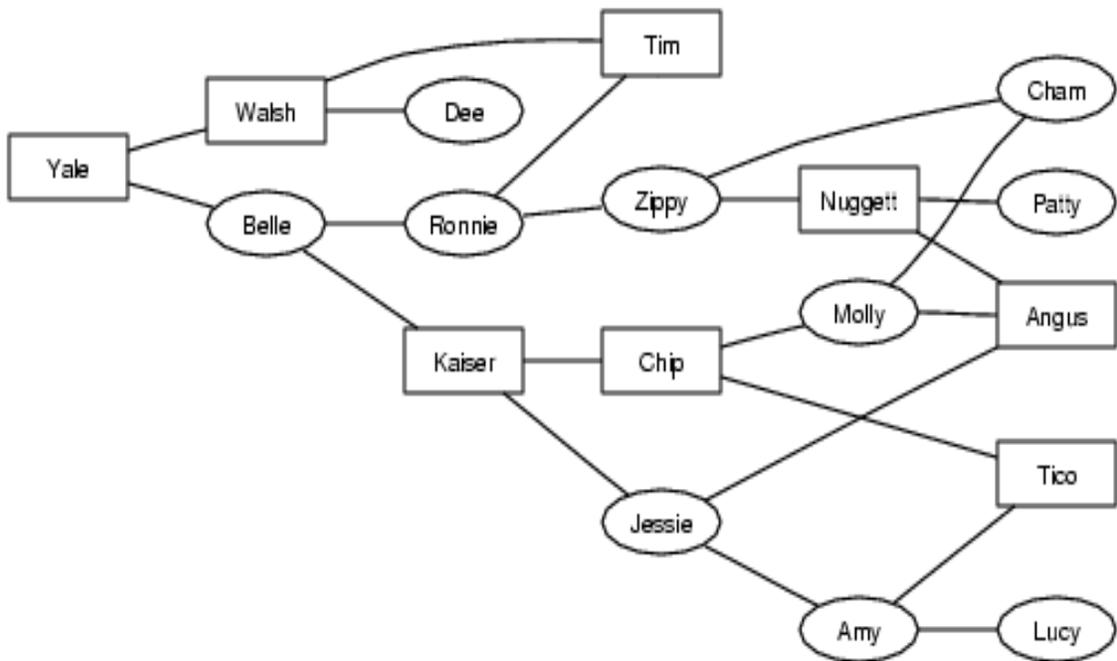
Appendix Figure 2.9. Gaelic ( $r_{\text{breed}} = 0.268$ ;  $f = 0.227$ )



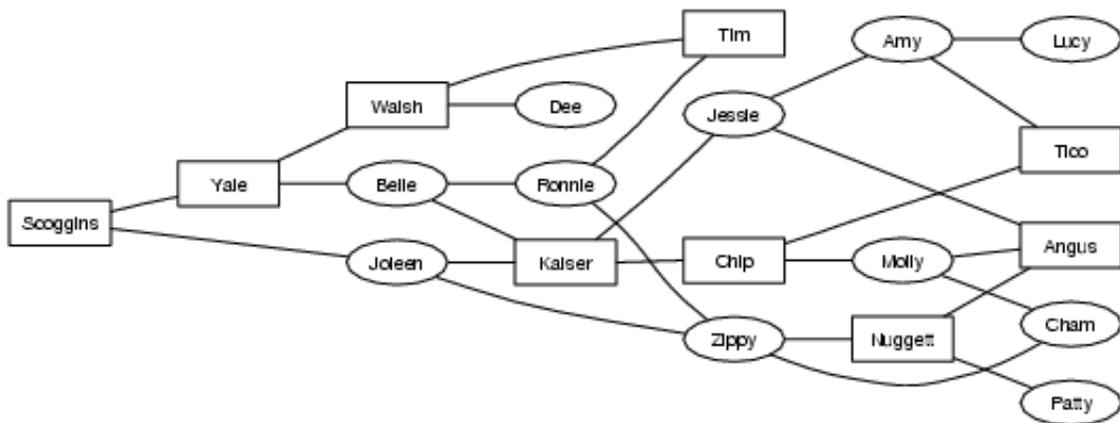
Appendix Figure 2.10. Lynne ( $r_{\text{breed}} = 0.267$ ;  $f = 0.208$ )

## **APPENDIX 3**

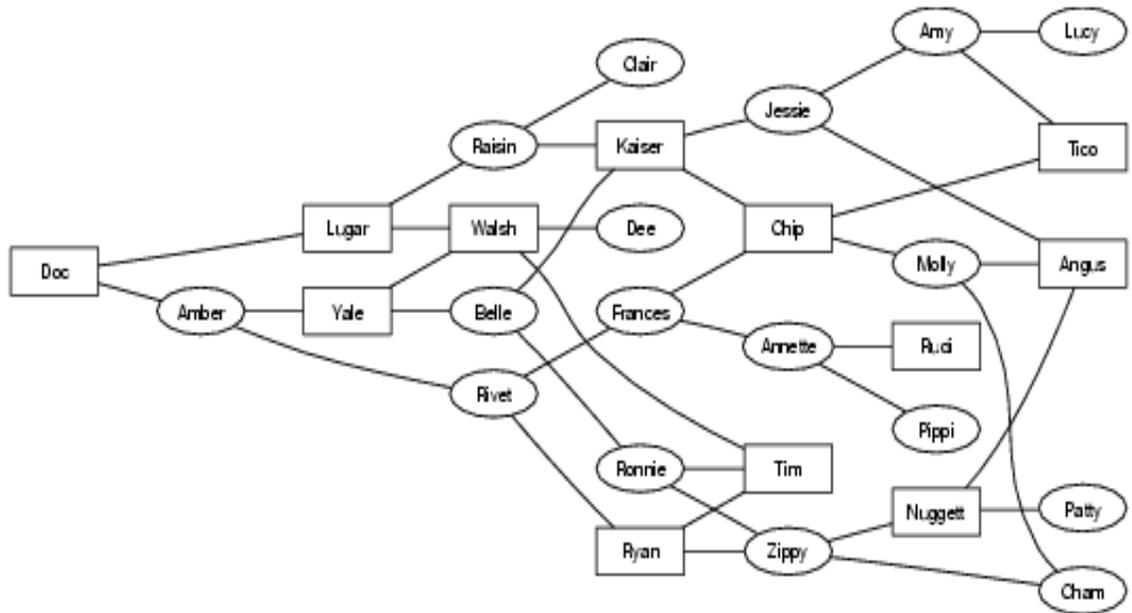
### **PEDIGREES OF THE TEN LABRADOR RETRIEVER SIREs WITH THE HIGHEST AVERAGE COEFFICIENT OF RELATIONSHIP TO THE BREED**



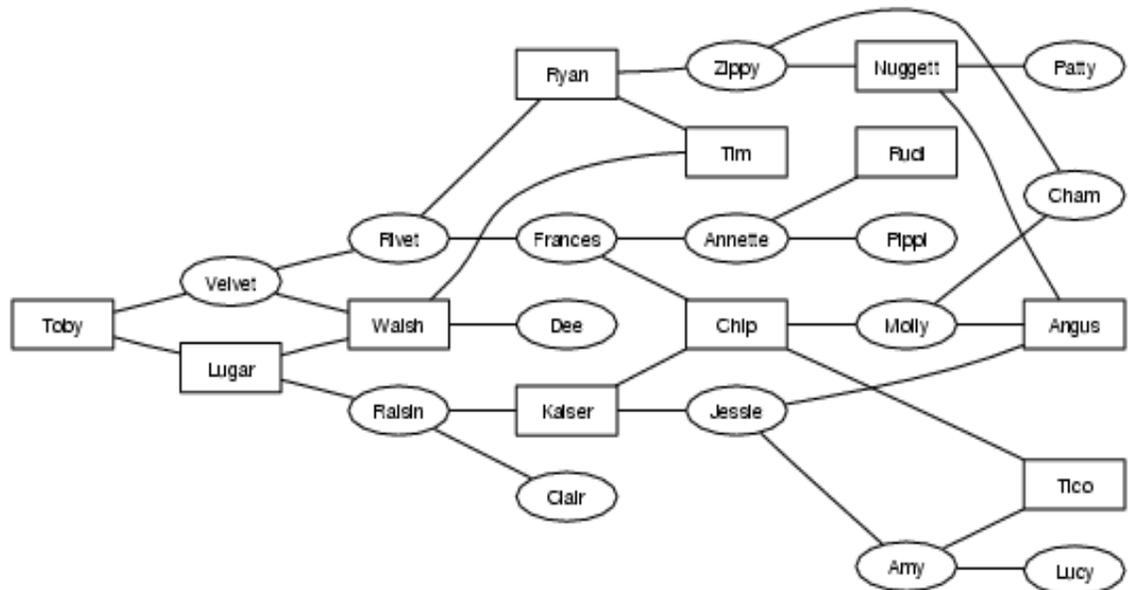
**Appendix Figure 3.1.** Yale ( $r_{\text{breed}} = 0.249$ ;  $f = 0.062$ )



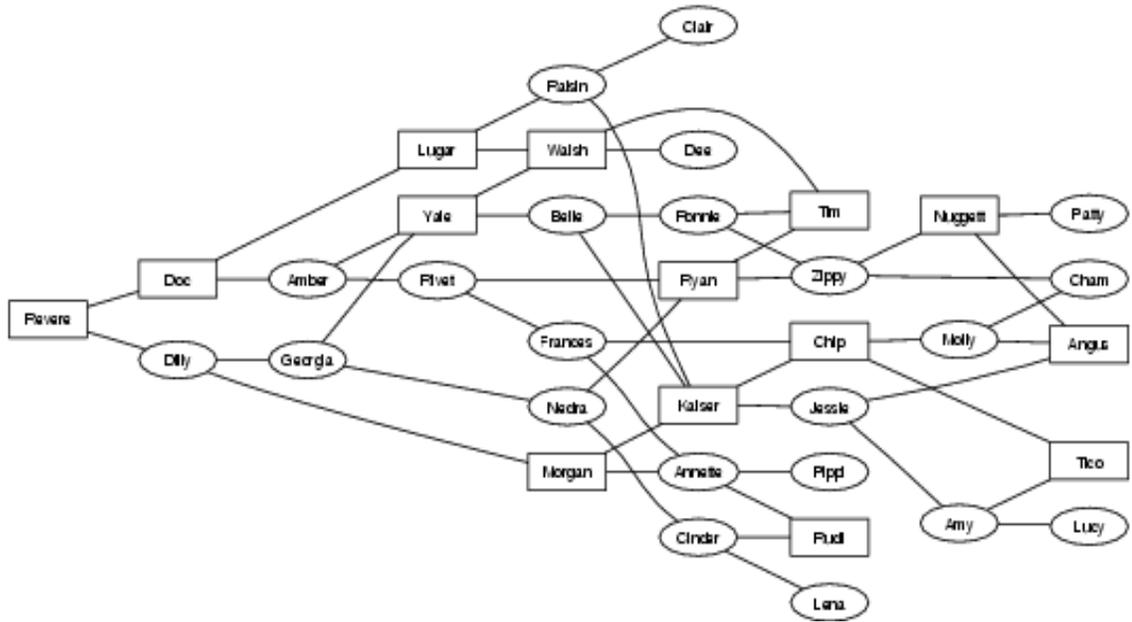
**Appendix Figure 3.2.** Scoggins ( $r_{\text{breed}} = 0.239$ ;  $f = 0.116$ )



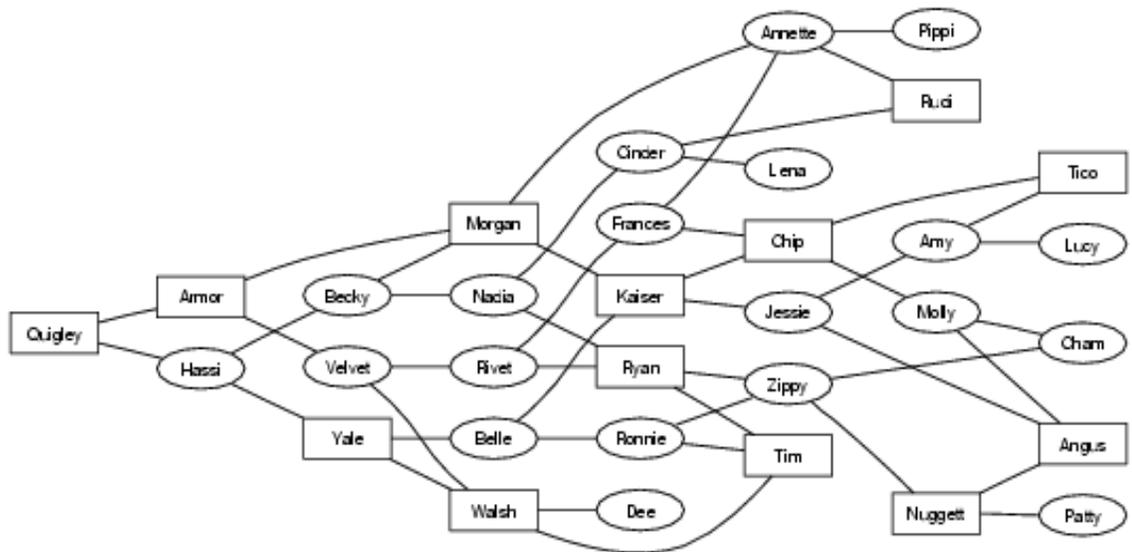
**Appendix Figure 3.3.** Doc ( $r_{\text{breed}} = 0.234$ ;  $f = 0.117$ )



**Appendix Figure 3.4.** Toby ( $r_{\text{breed}} = 0.227$ ;  $f = 0.153$ )

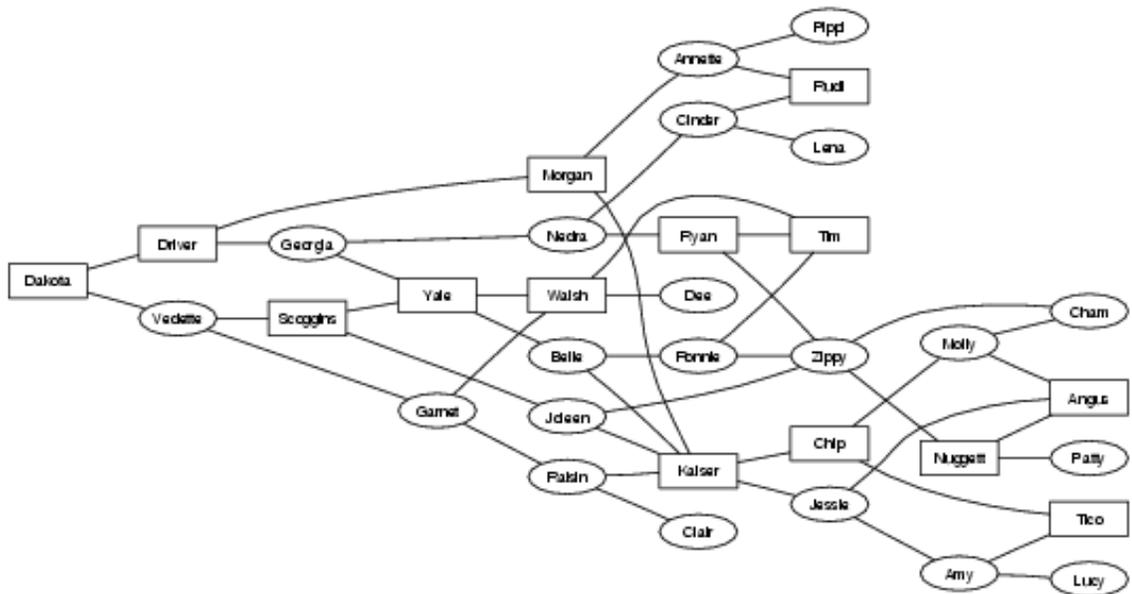


Appendix Figure 3.5. Revvere ( $r_{\text{breed}} = 0.223$ ;  $f = 0.120$ )

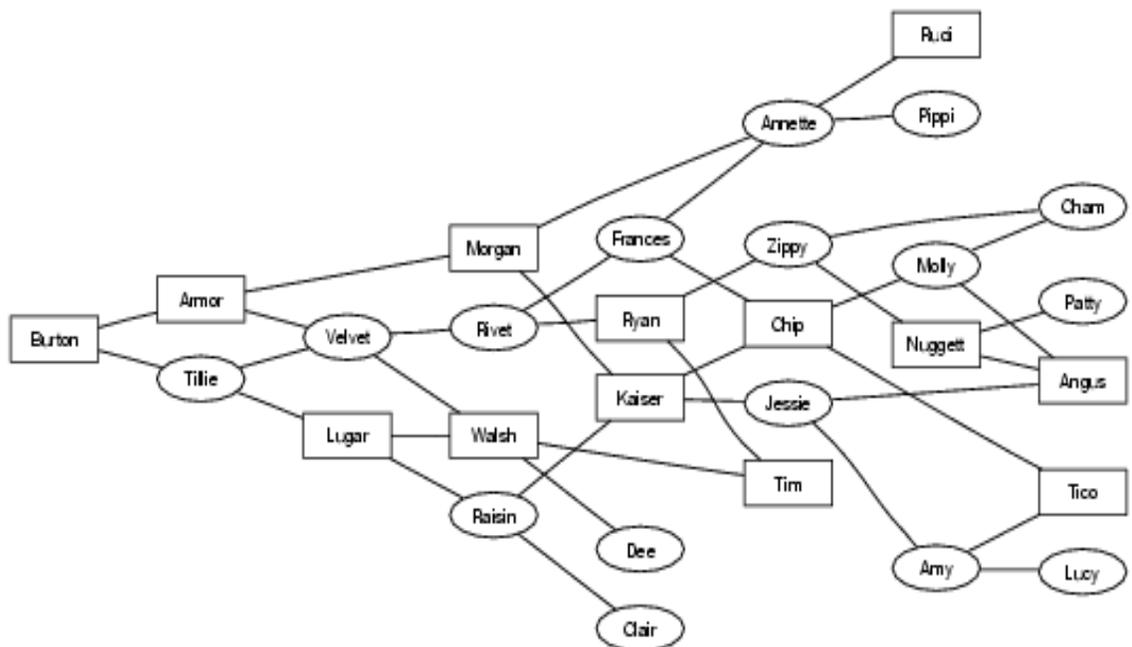


Appendix Figure 3.6. Quigley ( $r_{\text{breed}} = 0.222$ ;  $f = 0.153$ )





Appendix Figure 3.9. Dakota ( $r_{\text{breed}} = 0.220$ ;  $f = 0.123$ )

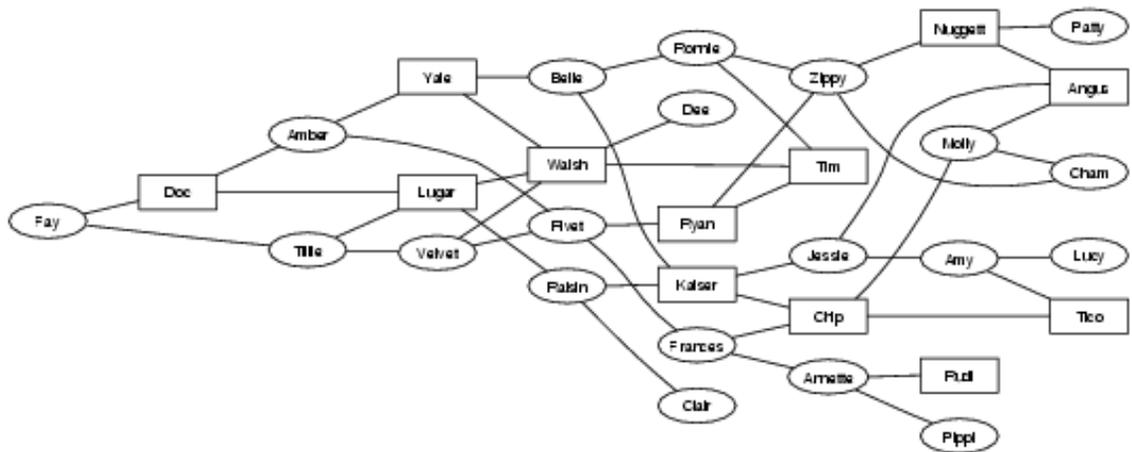


Appendix Figure 3.10. Burton ( $r_{\text{breed}} = 0.220$ ;  $f = 0.203$ )

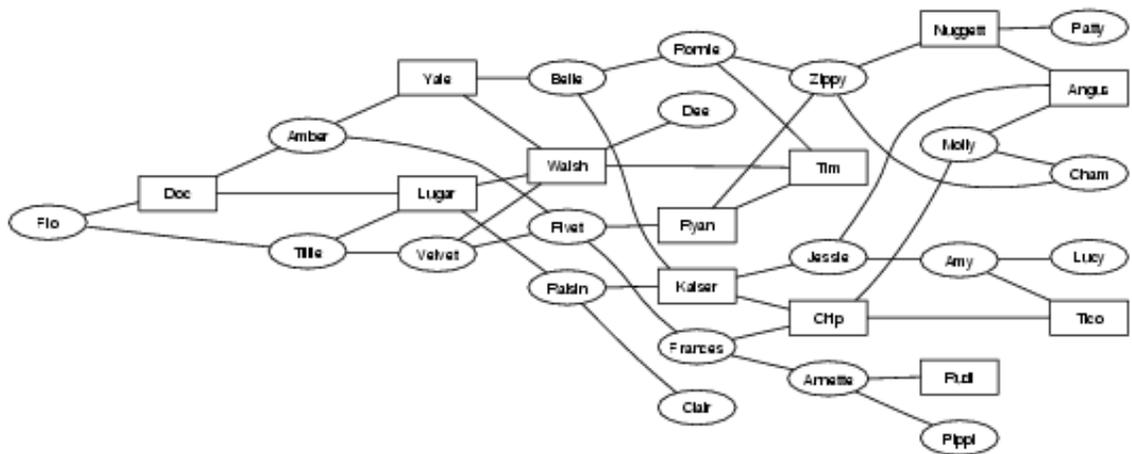
## **APPENDIX 4**

### **PEDIGREES OF THE TEN LABRADOR RETRIEVER DAMS WITH THE HIGHEST AVERAGE COEFFICIENT OF RELATIONSHIP TO THE BREED**

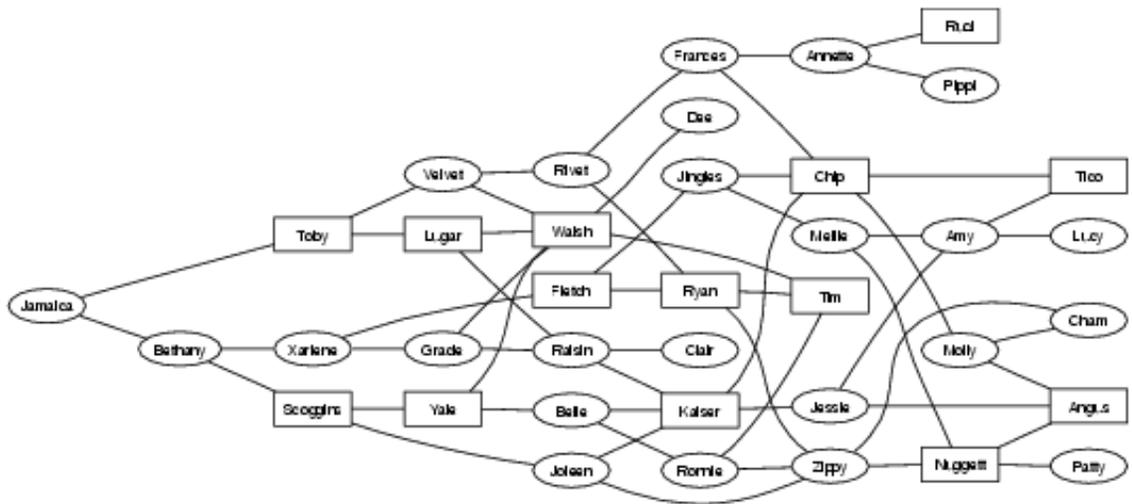




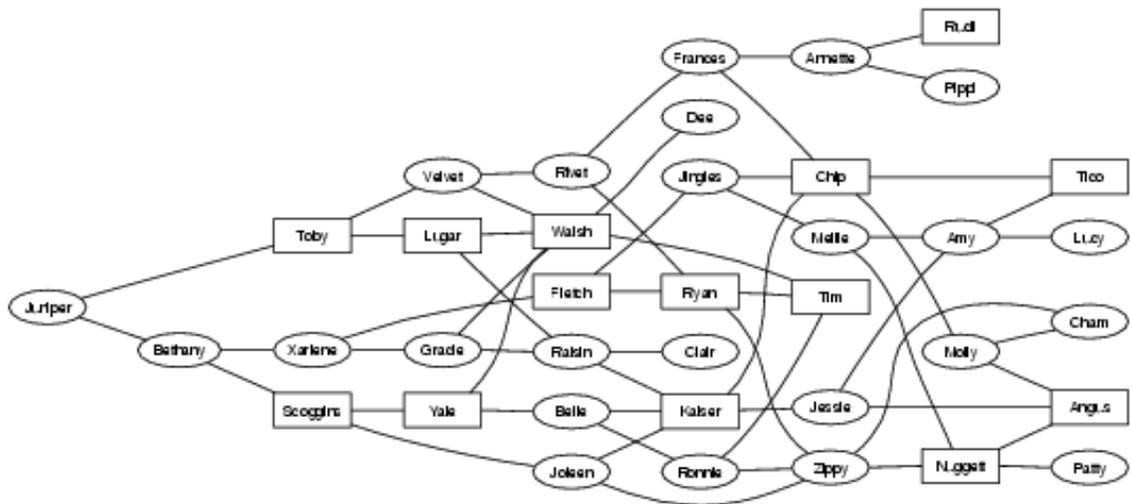
Appendix Figure 4.3. Fay ( $r_{\text{breed}} = 0.228$ ;  $f = 0.252$ )



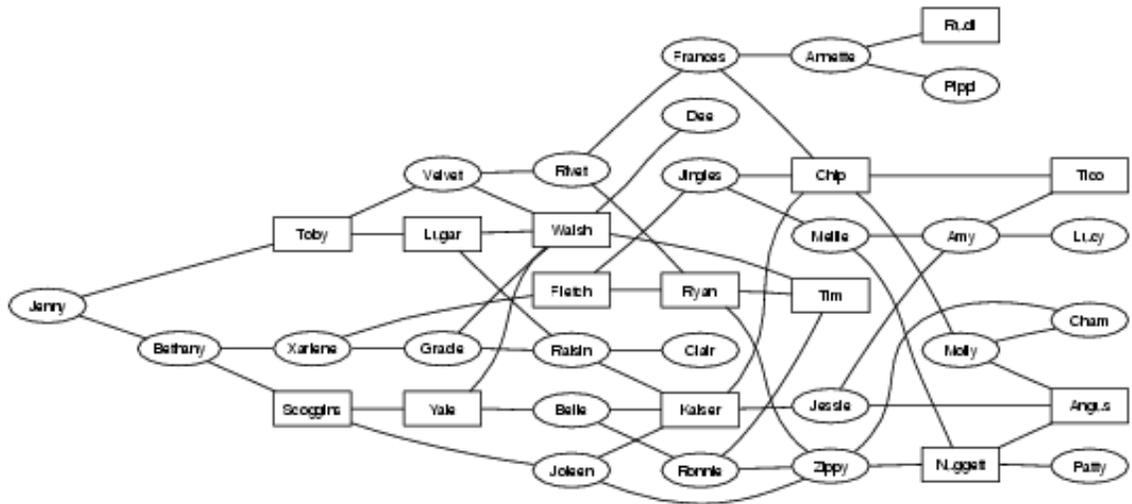
Appendix Figure 4.4. Flo ( $r_{\text{breed}} = 0.228$ ;  $f = 0.252$ )



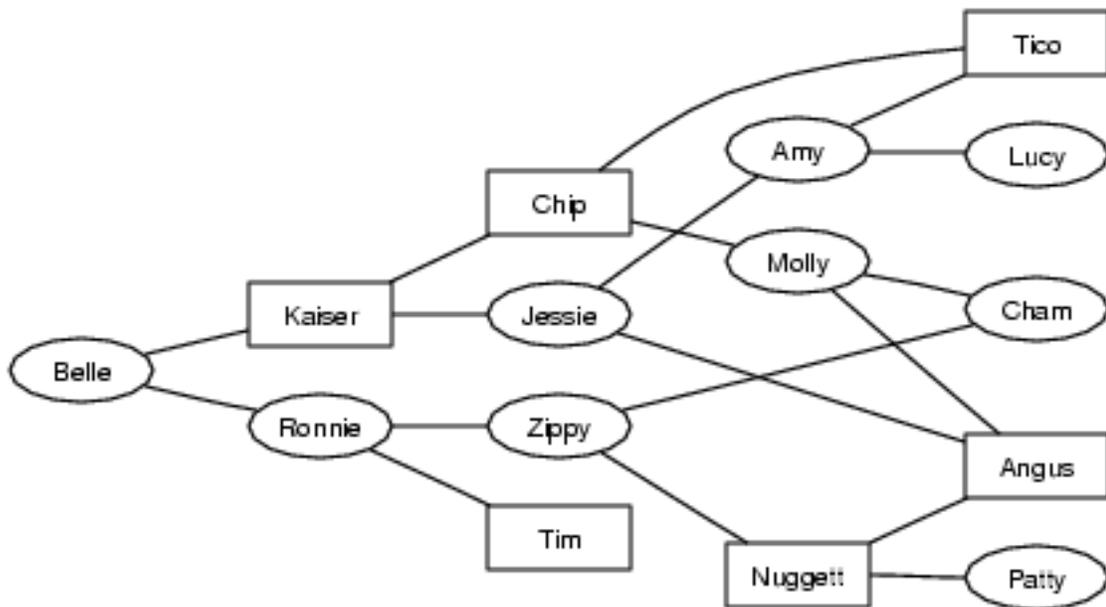
Appendix Figure 4.5. Jamaica ( $r_{\text{breed}} = 0.228$ ;  $f = 0.137$ )



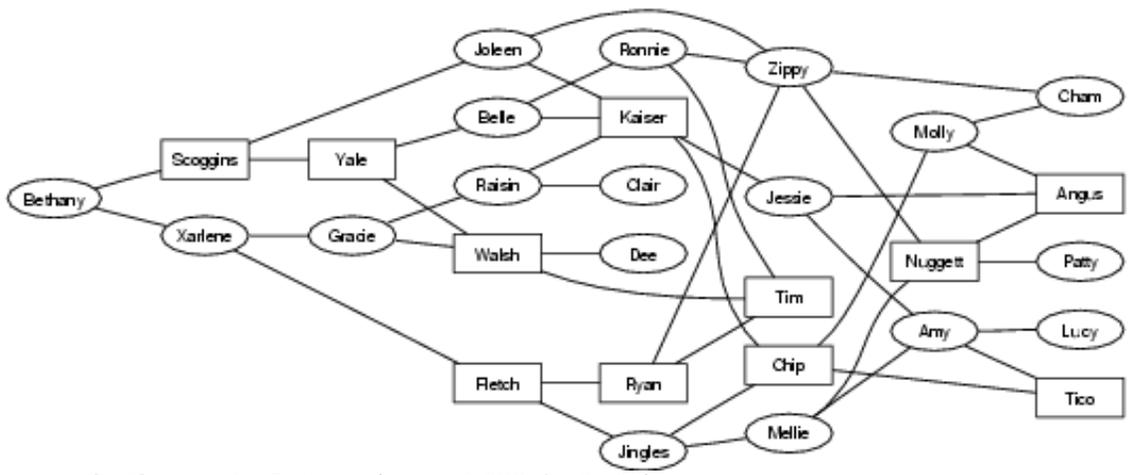
Appendix Figure 4.6. Juniper ( $r_{\text{breed}} = 0.228$ ;  $f = 0.137$ )



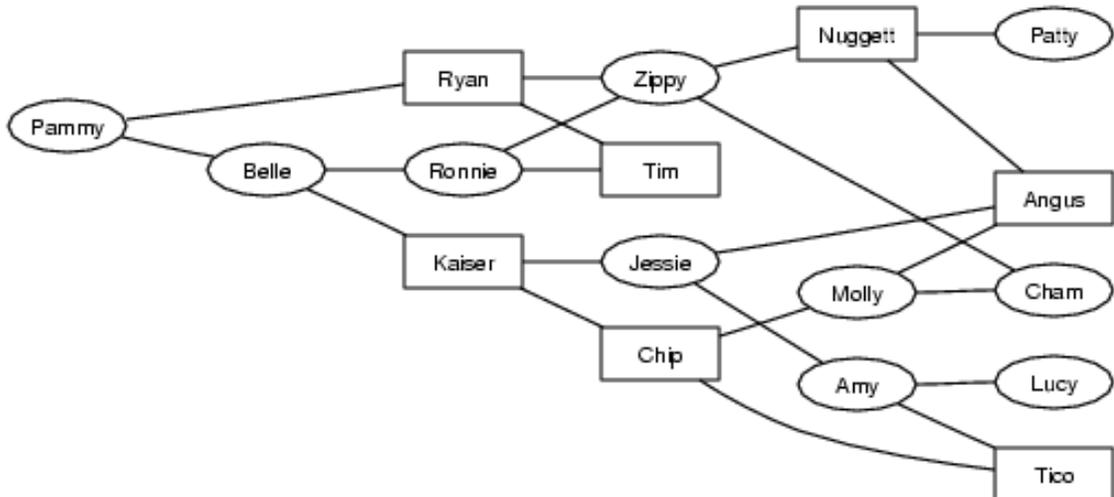
Appendix Figure 4.7. Jenny ( $r_{\text{breed}} = 0.227$ ;  $f = 0.137$ )



Appendix Figure 4.8. Belle ( $r_{\text{breed}} = 0.226$ ;  $f = 0.039$ )



Appendix Figure 4.9. Bethany ( $r_{\text{breed}} = 0.226$ ;  $f = 0.129$ )



Appendix Figure 4.10. Pammy ( $r_{\text{breed}} = 0.224$ ;  $f = 0.145$ )

## VITA

John B. Cole was born July 17, 1972, in Lake Charles, Louisiana, to Craig and Marie Cole. He was raised in Lafayette, Louisiana, and graduated from the Louisiana School for Math, Science and the Arts in Natchitoches, Louisiana, in May, 1990. He attended Louisiana State University and received the Bachelor of Science Degree in animal systems (Dairy Production) with a minor in microbiology in May, 1994. He entered the graduate program in Animal, Dairy and Poultry Sciences at LSU and received the Master of Science degree with a minor in applied statistics in August, 1996. He pursued further graduate work at the University of Minnesota under the supervision of Dr. L. B. Hansen before entering the doctoral program at LSU in June, 2000. He married Misty J. Millen on July 7, 2001. John and Misty are the proud parents of Clothilde, a four-breed composite dog and Mike the Tiger, an orange tabby cat. He will receive the degree of Doctor of Philosophy at the May 2003 Commencement ceremony.