

Comparative Longevity of Pet Dogs and Humans: Implications for Gerontology Research

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The effect of breed and body weight on longevity in the pet dog was analyzed, and a method was developed to standardize the chronological age of dogs in terms of physiological time, using human year equivalents. Mortality data from 23,535 pet dogs were obtained from a computerized data base of North American veterinary teaching hospitals, and the median age at death was determined for pure and mixed breed dogs of different body weight. Body size in the dog was inversely related to longevity. Within each body weight category, the median age at death was lower for pure breed dogs compared with mixed breed dogs. The difference between the standardized physiological ages of mixed breed dogs of the same chronological age in the smallest and largest body weight categories varied from 8 to >15 years, and between large and small pure breed dogs, the disparity was even greater. Laboratory research to explore the biological basis for these breed and body weight specific differences in life span among dogs may provide additional clues to genetic factors influencing senescence.

THE dog (*Canis familiaris*) is one of the primary species of mammals used for comparative biomedical research (National Academy of Sciences, 1981; USDA, 1994). In addition, an estimated 52.5 million dogs are kept as family pets in 36% of American households (AVMA, 1993). As a result of thousands of years of domestication and selective breeding for behavior, working ability, temperament, and phenotypic characteristics such as coat color and length, body size, and facial features, there are nearly 400 recognized dog breeds (Wilcox and Walkowicz, 1991), and the normal adult body weight varies over 100-fold between the smallest and largest pure breed dogs. For example, the adult Saint Bernard can exceed 200 lbs body weight, while the adult Chihuahua may weigh as little as 1–2 lbs (Wilcox and Walkowicz, 1991). This large range in body weight is associated with considerable variation in life span, despite apparent similarities in physiology, diet, and environment. The average life span among dog breeds varies by a factor of >2 among different breeds, e.g., Great Dane, 5–8 years, vs Miniature Poodle, 10–14 years (Clark and Steiner, 1983). Life tables have been constructed for laboratory Beagles (National Academy of Sciences, 1981), but are lacking for most other pure or mixed breed dogs. However, there is substantial empirical information indicating that life span in dogs is inversely related to body size (Comfort, 1960, 1961, 1964; Mather, 1971; Mosier, 1981; National Academy of Sciences, 1981; Clark and Steiner, 1983; Reif, 1983; MacDougall and Barker, 1984; American Kennel Club, 1985; Wilcox and Walkowicz, 1991). Recently, giant pure breed dogs were shown to die at a younger age than small pure breed dogs (Deeb and Wolf, 1994; Li et al., 1996). In a study of pet dogs, cellular proliferative capacity was correlated with age in several small breeds of dogs and with body size in two large breeds (Li et al., 1996).

This inverse relationship between life span and body size in dogs is opposite to the positive relationship observed

among different mammalian species such as the elephant (70 years) and the rat (5 years) (Comfort, 1961; Kirkwood, 1992). Although a similar inverse relationship has been noted within humans (Samaras and Storms, 1992) and laboratory rats (Nohynek et al., 1993), in no other species is this inverse relationship so obvious. To our knowledge, the biological basis for this inverse relationship between size and life span in the dog has not been explained.

The positive relationship between body weight and life span among mammals has been attributed to differences in metabolic rate and the rate of maturation or growth (Finch, 1990; Frolkis and Muradian, 1991; Sohal and Weindruch, 1996). The mechanism by which metabolic rate affects life span is unclear, but it is likely that smaller animals with higher metabolic rates are under relatively higher levels of oxidative stress (Sohal and Weindruch, 1996). In a study of six mammalian species (mouse, rat, guinea pig, rabbit, pig, cow), there was no clear association between levels of antioxidant defenses (superoxide dismutase, catalase, glutathione) and life span, whereas mitochondrial rates of O₂ and H₂O₂ production were inversely correlated with life span (Sohal and Weindruch, 1996). Other interspecies comparisons have shown weak correlations between superoxide dismutase concentrations in liver, heart, and brain with life span (Finch, 1990). In the canine species, smaller dogs generally have a higher metabolic rate and a shorter period of physical maturation than larger dogs (Lindstedt and Calder, 1981; Lewis et al., 1987). It is unknown, however, whether there are breed and/or size-specific differences in antioxidant defenses or prooxidant levels in dogs, or whether such differences are associated with increased or decreased longevity.

Brain mass has been shown to be more strongly associated with life span than body mass among mammals (Sacher, 1959; Economos, 1980; Frolkis and Muradian, 1991), suggesting that increased life span was a consequence of greater intelligence, more reliable central neural regulation (Sacher,

1978; Frolkis and Muradian, 1991) or a greater neuron reserve (Finch, 1990). However, the neurobiological basis for a direct effect, if any, of increasing brain weight on longevity has not been established.

Life span and other physiological processes or "biological time periods" such as gestation, cardiac, and respiratory cycles, or the time to circulate blood volume among various warm-blooded animal species, may be relatively constant when compared in terms of physiological time (Adolph, 1949; Western, 1979; Lindstedt and Calder, 1981; Finch, 1990). The use of physiological time to define a variable time scale among animals of different sizes has been described (Lindstedt and Calder, 1981) and has been used to compare dog and human ages (Lebeau, 1953; Schneider, 1970; Albert et al., 1994). Lebeau recognized that the relationship between human age and dog age was not constant over the dog's life span, and could not be accurately described with a simple linear relationship (Lebeau, 1953). Using life-stage markers roughly equivalent to puberty, adulthood, old age, and maximum life span, he proposed a series of coefficients by which to multiply dogs' ages to determine the equivalent in human years. Although Lebeau's method has been described as the best presently available, it does not account for the influence of breed and body weight on longevity in the dog, and the need for an improved method has been recognized (National Academy of Sciences, 1981). Therefore, this study was conducted (1) to determine the relationship of breed and body weight to life span in dogs, and (2) to convert the chronological ages of dogs of different sizes and breeds into human equivalents (physiological ages), based on the relative life span of the two species, using a refinement of Lebeau's method.

METHODS

Study population. — Population-based epidemiologic studies on breed-specific disease rates or life spans in the pet dog have not been conducted. However, information on mortality among different breeds and sizes of dogs seen at veterinary teaching hospitals in the United States and Canada is available in the Veterinary Medical Data Base (VMDB). The VMDB was established by the National Cancer Institute in 1964 at the College of Veterinary Medicine, Michigan State University, to provide a reliable and standardized source of information on diseases of domestic animals. It was eventually expanded to include 20 American and 2 Canadian veterinary schools. The data base has information on species, sex, age, breed, weight, vital status, and diagnoses, and has been used to examine mortality among purebred dogs of different sizes (Deeb and Wolf, 1994; Li et al., 1996). The records of all dogs ≥ 1 year of age that died or were euthanatized for reasons other than trauma or poisoning from 1980–1990 were obtained in electronic format from the VMDB. Dogs whose deaths were related to trauma or poisoning were excluded, because these conditions would represent premature events caused primarily by environmental insults, and would only minimally reflect the influence of physiological processes on longevity.

Median age at death. — Data for age and weight are recorded as categorical variables in the VMDB, e.g., 1–<2

years, 2–<4 years, 4–<7 years, 7–<10 years, 10–<15 years, and ≥ 15 years; and 15–29 lbs, 30–49 lbs, 50–74 lbs, 75–100 lbs, and >100 lbs. Descriptive statistics were generated using the Statistical Analysis System for Windows (SAS), Version 6.11. A graphical method was used to determine the median age at death for both mixed (Figure 1) and pure breed dogs, and for dogs within weight categories. First, because data for age were categorical, the midpoints of the six age categories were plotted on the x-axis (age of dog at death), and the cumulative percent of dogs on the y-axis. A horizontal line was drawn from the 50% point on the y-axis, and a vertical line was drawn to the x-axis from the point where the horizontal line intersected the cumulative mortality curve. The point where the vertical line intersected the x-axis was considered to be the median age at death for a given weight or breed of dog. The median ages at death for pure and mixed breed dogs within each weight group were compared using the Wilcoxon rank sum test and across weight groups using the Kruskal-Wallis test (Schott, 1990).

Physiological age. — Lebeau's (1953) published estimates for comparing human and dog ages were plotted, and a third-degree polynomial curve was fit to the data using Microsoft EXCEL software (Figure 2). The human equivalent of the median age at death for all mixed breed dogs in the VMDB was then determined graphically. Vertical lines were drawn up to the polynomial curve from two points on the x-axis: the median age at death (8.5 years) and twice the median age at death (17 years) for all mixed breed dogs. Horizontal lines were drawn from the intersections of these two vertical lines with the polynomial curve to the y-axis. The two points where the horizontal lines intersected the y-axis (51 years and 84 years) were the human age equivalents of the median and twice the median age at death, respectively, of all mixed breed dogs.

Polynomial curves relating human age to dog age were constructed for different sizes of dogs using the curve in Figure 1 as a starting point. For each of the five weight groups of mixed breed dogs, the curve in Figure 1 was

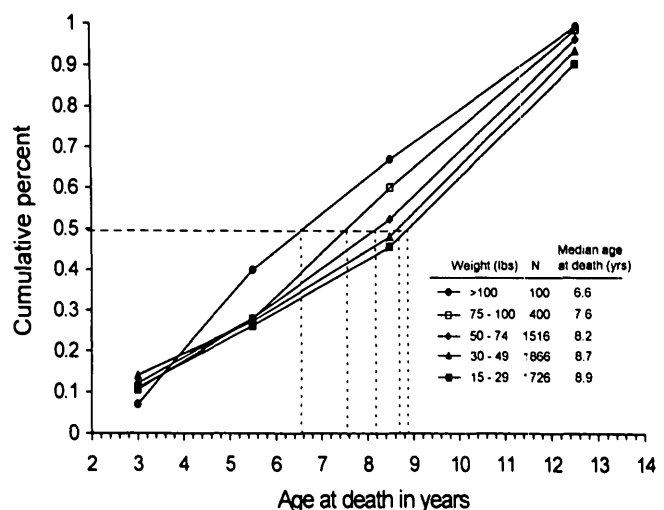


Figure 1. Median age at death, by body weight, of mixed breed dogs in the Veterinary Medical Data Base from 1980–1990.

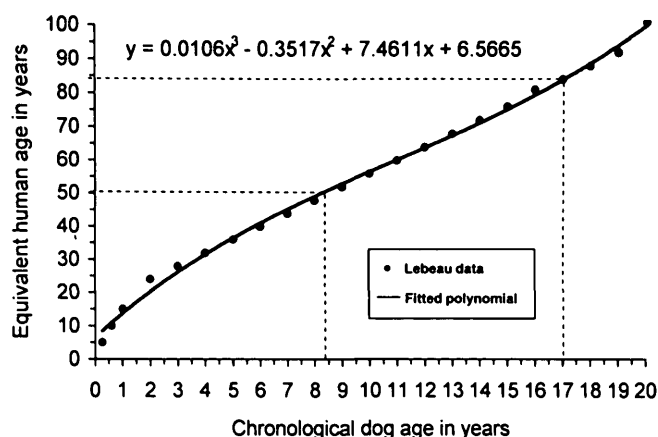


Figure 2. Plot of dog ages and their human age equivalents based on Lebeau's (1953) model.

modified such that each new curve passed through these two points: the intersection of a vertical line from the median age at death for that weight group on the x-axis and a horizontal line from 51 years of age on the y-axis, and the intersection of a vertical line from twice the median age at death for that weight group on the x-axis and a horizontal line from 84 years of age on the y-axis (Figure 3). The formulas corresponding to each of these five fitted polynomial curves were obtained using Microsoft EXCEL (see Appendix).

Because of different median ages at death for different weight groups of mixed breed dogs, the cubic, square, and linear coefficients for dog age were different for each of the five polynomial equations. In order to develop a general formula for equating human and dog years that was applicable to each weight category, the relationship between these coefficients and the median age at death was determined. The cubic, squared, and linear regression coefficients and the constant terms in the five polynomial equations were separately regressed on the median age at death. The four resulting regression equations that now incorporated the median age at death were then substituted as the coefficients and the constant term in the polynomial formula to standardize dog age to human age (see Appendix for details).

RESULTS

Study population. — The records of 38,006 dogs ≥ 1 year of age that died or were euthanatized from 1980–1990 were obtained, including 9,041 (23.8%) mixed breed dogs and 28,965 (76.2%) pure breed dogs. Weight was not recorded for 9,561 (25.1%) dogs. Dogs weighing <15 lbs (N = 4910, 12.9%) were excluded because they were thought to represent too broad a weight category, i.e., a 14-fold difference in body weight. In the final analysis, there were a total of 5,608 mixed breed and 17,927 pure breed dogs.

Median age at death. — The median age at death was 8.5 years for all mixed breed dogs and 6.7 years for all pure breed dogs. The median ages at death were 8.9, 8.7, 8.2, 7.6, and 6.6 years for mixed breed dogs (Figure 1), and 7.6, 6.0, 6.4, 6.6, and 5.4 years for pure breed dogs in the 15–29,

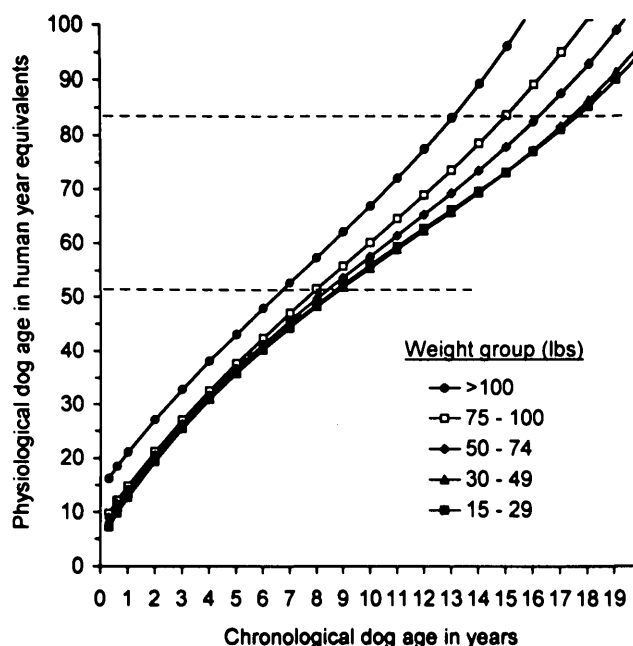


Figure 3. Polynomial curves fitted to Lebeau's (1953) model for comparing dog ages and human ages, by body weight. (See Appendix for more information.)

30–49, 50–74, 75–100, and > 100 lbs weight categories, respectively. For each weight group, the age at death of pure breed dogs was significantly ($p = .0001$) less than that for mixed breed dogs.

Evaluation of Lebeau's model. — The third-degree polynomial curve fitted to Lebeau's suggested human and dog age equivalents ($y = .0106X^3 - .3517X^2 + 7.4611X + 6.5665$) was visually judged to be a good fit (Figure 2). Use of a third-degree polynomial allowed for a relatively greater increase in human age at both younger and older extremes of dog ages.

Dog physiological age and human equivalent. — The five fitted polynomial curves for determining the physiological age of dogs in human equivalents are shown in Figure 3. The polynomial curve for Lebeau's original suggested equivalents fell between the curve for 30–49 lb mixed breed dogs and the curve for 50–74 lb mixed breed dogs (not shown). The general formula for standardizing dog age, or physiological age (PA) of the dog, in human years is:

$$PA = \{[(-.0013 \times X) + .0221] C^3\} + \{[(X \times -.0285) - .1071] C^2\} + \{[(.2911 \times X) + 4.9979] C\} + (-3.6437 \times X) + 37.423$$

where X = median age at death for the size or breed of dog in the VMDB, and C = chronological age of dog, in years.

The values for physiological age derived from the fitted polynomial curves (Figure 3) were nearly identical to the values obtained from the single general polynomial equation (Table 1). The calculated physiological times in human year equivalents for each one year of chronological time for dogs, for each of the five dog weight categories, are presented in Table 2. Median ages at death of the most common pure

breed dogs in the VMDB are presented in Table 3, and the physiological ages in human year equivalents for selected pure breed dogs are shown in Table 4. The results of the age standardization procedure indicate that the differences in physiological age compared with chronological age were

substantial. For example, for dogs 10 years of age, the age difference in human year equivalents between the largest and smallest dogs was over 11 years, and a one-year chronological interval in dog age ranged from 3.5 to 5.2 years in physiological time.

Table 1. Physiological Age of Mixed Breed Dogs, in Human Years, According to the Dog's Chronological Age and Body Weight

Chronological Age of Dog (years)	Dog Weight (lbs)				
	15-30	30-50	50-75	75-100	>100
0.25	6.8	7.6	9.3	11.5	15.1
0.6	9.4	10.1	11.8	13.9	17.4
1	12.2	12.9	14.6	16.6	20.0
2	18.8	19.4	21.0	22.9	26.1
3	24.8	25.4	26.9	28.8	31.8
4	30.2	30.8	32.3	34.2	37.2
5	35.2	35.8	37.4	39.2	42.3
6	39.8	40.4	42.0	44.0	47.2
7	44.0	44.7	46.4	48.5	52.0
8	48.0	48.8	50.7	52.9	56.7
9	51.7	52.6	54.7	57.3	61.6
10	55.3	56.3	58.7	61.7	66.6
11	58.8	59.9	62.8	66.1	71.8
12	62.3	63.6	66.8	70.7	77.2
13	65.8	67.3	71.1	75.6	83.1
14	69.4	71.2	75.5	80.8	89.5
15	73.2	75.2	80.2	86.3	96.4
16	77.2	79.5	85.3	92.3	103.9
17	81.5	84.1	90.8	98.8	112.1
18	86.1	89.2	96.8	105.9	121.1
19	91.2	94.7	103.3	113.7	131.0
20	96.7	100.6	110.5	122.2	141.9

Body weight and longevity within individual pure breeds. — It was assumed that the size of dogs was accurately reflected by their body weight category in the VMDB. Since a dog's weight category in the VMDB was based on its actual body weight, obesity or cachexia could have resulted in dogs being assigned to a different weight category than if their ideal or normal body weight was used. There were four breeds in which the weight of individual dogs fell in >2 weight categories and for which there was a sufficient sample size to examine the relationship of body size with longevity (Doberman Pinscher, German Shepherd, Golden Retriever, and Labrador Retriever). Within each of these breeds, there was no apparent trend for increasing body weight to be associated with decreased median age at death (data not shown).

Manner of death and median age at death. — The ages of dogs that were euthanatized were compared to the ages of dogs that died naturally in order to determine if dogs that were euthanatized died prematurely, and the magnitude of this effect, if any, on the median age at death. Overall, 68.5% of pure breed dogs and 70.2% of mixed breed dogs were euthanatized, and the proportion of pure and mixed breed dogs that were euthanatized was similar in each weight category. For mixed breed dogs, the median age at death was higher for dogs that were euthanatized than for dogs that died naturally in all of the weight groups except those dogs > 100 lbs (data not shown), thus confirming that euthanasia did not artificially decrease the median age at death in dogs in the VMDB.

Table 2. Influence of Body Weight on Physiological Age, in Human Years, for Each Chronological Age Interval in Mixed Breed Dogs

Chronological Dog Age Interval (years)	Dog Weight (lbs)					Lebeau Curve*
	15-30	30-50	50-75	75-100	>100	
1-2	6.6	6.5	6.4	6.3	6.1	6.5
2-3	6.0	6.0	5.9	5.8	5.7	5.9
3-4	5.5	5.4	5.4	5.4	5.4	5.4
4-5	5.0	5.0	5.0	5.0	5.1	4.9
5-6	4.6	4.6	4.7	4.8	4.9	4.6
6-7	4.2	4.3	4.4	4.6	4.8	4.2
7-8	4.0	4.0	4.2	4.4	4.8	4.0
8-9	3.7	3.8	4.1	4.4	4.8	3.8
9-10	3.6	3.7	4.0	4.4	5.0	3.7
10-11	3.5	3.6	4.0	4.5	5.2	3.6
11-12	3.5	3.7	4.1	4.6	5.5	3.6
12-13	3.5	3.7	4.2	4.9	5.9	3.6
13-14	3.6	3.8	4.4	5.2	6.3	3.8
14-15	3.8	4.0	4.7	5.5	6.9	4.0
15-16	4.0	4.3	5.1	6.0	7.5	4.2
16-17	4.3	4.6	5.5	6.5	8.2	4.5
17-18	4.6	5.0	6.0	7.1	9.0	4.9
18-19	5.1	5.5	6.5	7.8	9.9	5.3
19-20	5.5	6.0	7.2	8.5	10.8	5.8

*Human age equivalents calculated from a polynomial curve fit to Lebeau's estimates.

Source: Lebeau, 1953.

Table 3. Mean Age at Death of the Most Common Breeds of Dogs in the VMDB From 1980–1990*

Dog Breed	Number of Dogs	Median Age at Death (years)
Afghan	151	6.7
Airedale	164	6.5
Basset	283	6.3
Beagle	417	6.6
Boston Terrier	256	8.5
Boxer	455	6.0
Brittany Spaniel	239	7.0
Bulldog	196	4.6
Cocker Spaniel	775	5.6
Collie	431	7.5
Dachshund	829	5.5
Dalmatian	164	6.2
Doberman Pinscher	1522	5.9
English Setter	197	7.0
German Shorthaired Pointer	173	7.2
German Shepherd	1793	6.8
Golden Retriever	1088	6.6
Great Dane	487	4.6
Irish Setter	537	7.5
Labrador Retriever	1113	6.2
Lhasa Apso	225	5.4
Malamute	162	6.2
Old English Sheepdog	263	6.9
Pekingese	228	6.8
Miniature Poodle	1136	9.3
Standard Poodle	274	9.1
Rottweiler	185	3.5
Saint Bernard	307	5.8
Samoyed	214	7.1
Schnauzer	636	8.2
Scottish Terrier	238	8.5
Sheltie	477	7.5
Shih-Tzu	156	5.0
Siberian Husky	252	6.4
Springer Spaniel	308	6.3
Weimaraner	147	7.6
West Highland White Terrier	189	8.2

*Dogs that died < 1 year of age or that died due to poisoning or trauma were excluded.

DISCUSSION

This study extended the results of another study of 13 breeds of dogs in the VMDB (Deeb and Wolf, 1994); it demonstrated an inverse relationship between adult body weight and median age at death for both pure and mixed breed dogs in a hospital population, and confirmed empirical evidence for a similar relationship between larger body size and decreased life span in the pet dog population. A method was developed for standardizing the ages of dogs of different sizes and breeds, based on Lebeau's comparison of dog and human ages, using the relative longevity of dogs in a hospital population.

The difference between the physiological ages of mixed breed dogs of the same chronological age in the smallest and largest body weight categories varied from 8 to >15 years, and for large and small pure breed dogs, the disparity was even greater. These breed- and body weight-related differ-

ences in physiological age are important to consider when comparing dogs to other species and to each other, e.g., in clinical trials to evaluate new therapies in dogs when the outcome measure is a time-dependent variable such as survival time, time to tumor recurrence, or time to remission.

One advantage of the method used in this study is that human age provides a convenient and intuitive benchmark to standardize the chronological age of dogs in terms of physiological time. Although other species could be used as a standard, from a comparative perspective the choice of humans as a reference has advantages, because the dog is used as a model for a variety of human diseases and in clinical trials of chemotherapeutic agents. Using the method of age-standardization developed in this study, the physiological age at prostate cancer diagnosis was found to be similar in dogs and humans (Waters et al., 1996). Although most references in the literature for comparing dog and human ages ultimately refer to Lebeau's work in 1953 (Anonymous, 1954; Cairy, 1954; Schneider, 1970), another method has recently been used (Albert et al., 1994). In that study, the age at which only 10% of the population remained alive was used as the measure of life span in both dogs and humans, and ages were compared using a linear relationship (Albert et al., 1994). This resulted in a 1:5.5 year scaling for Beagle:men comparisons and a 1:5.8 year scaling for Beagle:women comparisons. However, using this linear relationship and normalizing to the 50% survival point resulted in 25% of the female dogs surviving beyond the human age equivalent of 100 years, which is inconsistent with human survival patterns (Albert et al., 1994). The age of a 16-year-old Beagle would be equivalent to an 88–92-year-old human using this linear scaling, vs 104 years using the method developed here. These discrepancies are a consequence of using a linear, rather than a polynomial, curve to standardize dog ages. A polynomial relationship allows for the human year equivalents for dogs' ages to be larger during growth and smaller during maturity. However, larger dogs require more time to physically mature than smaller dogs, yet they have a shorter life span. Thus, the physiological ages or human year equivalents calculated using this method may not be applicable when comparing growth rates or the time to physical maturity across the two species. For example, a 1-year-old Great Dane is equivalent to a 26-year-old human in terms of life span, but has not yet reached its full growth potential.

Since many dogs in the VMDB were referred by private practitioners to the veterinary teaching hospitals that participate in the VMDB, their median ages at death were probably not representative, and were probably biased downward, compared with dogs in the general pet population. Information on weight and age in the VMDB is recorded in broad categories; exact body weights and ages were not available. Therefore, data for age and weight are somewhat imprecise, and misclassification is possible. However, dogs of different sizes, and mixed and pure breed dogs, were subject to the same degree of imprecision and/or misclassification in their body weights. Therefore, the median ages at death of dogs in the VMDB should not be systematically biased due to misclassification, should reflect the relative differences in life span among mixed and pure breed dogs of different

Table 4. Physiological Age in Human Years for Selected Pure Breed Dogs, According to a Dog's Chronological Age*

Chronological Dog Age (yrs)	Miniature Poodle	Schnauzer	Beagle	Irish Setter	Golden Retriever	Doberman Pinscher	Great Dane
1	10.9	14.6	20.0	16.9	20.0	22.4	26.8
2	17.5	21.0	26.1	23.3	26.1	28.3	32.5
3	23.6	26.9	31.8	29.1	31.8	34.0	37.9
4	29.0	32.3	37.2	34.5	37.2	39.3	43.2
5	34.0	37.4	42.3	39.5	42.3	44.4	48.4
6	38.5	42.0	47.2	44.3	47.2	49.4	53.6
7	42.7	46.4	52.0	48.9	52.0	54.4	58.9
8	46.5	50.7	56.7	53.3	56.7	59.4	64.3
9	50.0	54.7	61.6	57.7	61.6	64.6	70.1
10	53.4	58.7	66.6	62.2	66.6	70.0	76.3
11	56.6	62.8	71.8	66.7	71.8	75.7	83.0
12	59.7	66.8	77.2	71.4	77.2	81.8	90.3
13	62.8	71.1	83.1	76.4	83.1	88.4	98.2
14	65.9	75.5	89.5	81.6	89.5	95.6	106.9
15	69.2	80.2	96.4	87.3	96.4	103.4	116.5
16	72.6	85.3	103.9	93.4	103.9	112.0	127.1

*The median age at death of the breed in the VMDB and the general polynomial formula were used to standardize dog ages in human year equivalents. Since larger dogs require more time to physically mature than smaller dogs but have a shorter life span, the physiological ages or human year equivalents calculated using this method may not be applicable when comparing growth rates or the time to physical maturity across the two species.

sizes, and should represent a reasonable surrogate for relative longevity among all dogs. Because there was no information on the longevity of dogs in the nonhospitalized pet population, it was not possible to perform a life-table analysis to construct survival curves for dogs of different weights or breeds.

It is possible that treatable conditions for which euthanasia was selected as an option were over-represented for some pure breeds. If owners elected euthanasia instead of treatment, this could result in premature death and would bias downward the median age at death for that breed. This possibility was not supported by analysis of the data. The proportion of pure breed dogs that were euthanatized was similar to the proportion of mixed breed dogs. Furthermore, mixed breed dogs that were euthanatized tended to have a higher median age at death than mixed breed dogs in the same weight category that died naturally. These findings are consistent with a previous report in which no difference in the length of survival was observed between dogs with breast cancer that were euthanatized or that died naturally (Shofer et al., 1989). However, there may be unrecognized biases in veterinary teaching hospital-based data that explain the difference in longevity between mixed and pure breed dogs of the same body weight. Therefore, a conservative estimate of the equivalent human ages, or physiological ages, of pure breed dogs could be obtained by using the median age at death of mixed breed dogs in the same weight category.

Differences in husbandry practices are unlikely to account for the differences in longevity observed between pure and mixed breed dogs, and among dogs of different body weights in this study. All dogs in the VMDB were patients seen at veterinary teaching hospitals, where the cost of treatment is likely to be high and where most of the patients are referred by other veterinary practices. Therefore, most dogs in the VMDB are well-cared-for family pets or show dogs that have a history of regular veterinary care, routine

vaccinations for common canine infectious diseases, deworming, proper housing, and adequate nutrition. Dogs tend to eat similar foods, although small breed dogs are likelier to derive a greater proportion of their daily caloric intake from table or canned food, whereas large breed dogs consume a greater proportion of commercial dry food (Glickman et al., 1995). In any case, the size-related pattern in longevity described in these results clearly historically preceded the introduction of commercial dog foods for pet dogs, so variations in their diet would not account for the observed differences in longevity between small and large breed dogs.

The decreased life span of pure breed dogs compared with mixed breed dogs in all weight categories in this study suggests that selective breeding of dogs over time for phenotypic traits such as body size has accelerated physiological aging, independent of the effect of size alone. This is consistent with the concept of hybrid vigor in animal and plant species. Since there was no apparent association between median age at death and body weight within individual breeds of dogs, it suggests that the correlation found between body size and longevity in dogs reflected more strongly the genetic makeup of the dogs' breed than it did the size (i.e., body condition) of an individual dog. The breeding of purebred dogs has been linked strongly to fashion, and this may have served to increase and multiply injurious recessive mutations (Ott, 1996). Over 400 genetic diseases have been described in dogs (Smith, 1994). Although individual breeds of dogs may have a higher or lower incidence of particular diseases, there is no evidence to suggest that a size-related distribution of specific diseases is sufficient to explain the observed relationship between increased size and decreased longevity in the dog. By virtue of their shorter life span, and perhaps common mechanisms related to aging, the onset of most neoplastic and degenerative disease occurs at an earlier age in large breed dogs than in smaller breeds. Furthermore, breed-related genetics alone does not explain

the strong inverse relationship observed between size and longevity in mixed breed dogs. We feel this is true despite the fact that mixed breed dogs are by definition a heterogeneous category, with some dogs being first-generation pure-bred crosses while others are the progeny of mixed breed parents.

A challenge in biogerontology research is to identify the biological processes that determine senescence and, therefore, life span. It has been noted that modern experimental research on aging has largely lost its comparative focus, with most research on mammals involving two species (inbred rats and mice) chosen not for their properties vis à vis aging but for convenience (Austad, 1993). Austad lists four contributions that a comparative perspective can offer aging research: (1) hypotheses formulation and evaluation; (2) assessment of the generality of aging mechanisms; (3) isolation of key physiological or biochemical factors influencing aging; and (4) choosing models for specific senescence problems. In this context, the pet dog seems to be an ideal candidate for a comparative model of aging.

Epidemiologic studies of the pet dog population to detect departures from expected life span among breeds of similar body weight might help to identify new models of aging and suggest new hypotheses. Since dogs are genetically dissimilar to the species most commonly used in gerontology research, dogs could be used to assess the generality of aging mechanisms identified in other species. The search for genetic factors related to aging is facilitated in the dog model, because intraspecies comparisons (among dog breeds or dogs of different body weight) would eliminate some of the noise attributable to interspecies differences in genetic makeup. Mapping of the canine genome is currently underway to identify genes causing disease (Smith, 1994; Morris Animal Foundation, 1995). It is a logical extension of this research to investigate markers of aging, and to evaluate in the dog gerontogenes identified in other species.

In addition to gene mapping, laboratory research to explore differences among dogs of different body weights, and pure vs mixed breed dogs of the same body weight, for their sensitivity to DNA damage, efficiency of DNA repair (Finch, 1990; Frolkis and Muradian, 1991), effectiveness of antioxidant systems or rate of prooxidant generation (Finch, 1990; Frolkis and Muradian, 1991; Sohal and Weindruch, 1996), immune function (Jazwinski, 1996), rate of red blood cell senescence (Vacha, 1983), or cellular proliferation (Li et al., 1996) could illuminate some basic mechanisms of senescence. Since many of these techniques are relatively noninvasive, requiring only blood or tissue samples obtained during the course of normal veterinary care, the large and accessible population of pet dogs seen at veterinary clinics could be utilized for gerontology research. The feasibility of such an approach has been demonstrated (Li et al., 1996).

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Appendix

1. The following are the coefficients and constant terms from the equations for the five polynomial curves used for determining the physiological age of dogs in human years, that were fitted to Lebeau's estimates with Microsoft EXCEL (Figure 3):

The polynomial equations took the following form:

$$\begin{aligned} &\text{physiological age of dog in human year equivalents} \\ &= (\text{cubic coefficient} \times \text{dog chronological age in years}^3) \\ &+ (\text{squared coefficient} \times \text{dog chronological age in years}^2) \\ &+ (\text{linear coefficient} \times \text{dog chronological age in years}^1) \\ &+ \text{constant term.} \end{aligned}$$

Coefficients for Chronological Age of Dog in the Five Polynomial Equations

Dog Weight Group	Cubic Coefficient	Squared Coefficient	Linear Coefficient	Constant Term	Median Age at Death (yrs)
> 100 lbs	.0138	-.3060	6.9388	14.446	6.6
75-100 lbs	.0109	-.3095	7.2373	7.8798	7.6
50-74 lbs	.0107	-.3341	7.3119	7.2232	8.2
30-49 lbs	.0106	-.3552	7.3865	6.5665	8.7
15-29 lbs	.0105	-.3728	7.7595	5.2532	8.9

2. To develop a general formula for determining the physiological age of dogs for any breed, it was necessary to determine how the cubic, squared, and linear coefficients and constant terms in the five polynomial equations were related to the median age at death. The five values for each type of term (coefficient or constant) listed above were separately regressed on the median age at death for the five weight groups of mixed breed dogs. The following table shows the results of regressing the four sets of terms on the median age at death:

The values for y shown below were substituted as coefficients in a general polynomial equation that predicted human age equivalents for any breed of dog, providing that the chronological age of the dog and the median age of death in the VMDB for the breed or weight group was known: physiological age of dog (PA), in human years = $\{[(-.0013 \times X) + .0221] \times C^3\} + \{(X \times -.0285) - .1071\} \times C^2 + \{[(.2911 \times X) + 4.9979] \times C\} + \{-3.6437 \times X\} + 37.423$, where X = median age at death in the VMDB for pure breed dogs or for weight category for mixed breed dogs, and C = chronological age of dog, in years.

Independent Variable in Regression Equation (y*)	Resulting Equation	R ² for Regression
Cubic coefficients	$y_{\text{cubic}} = -0.0013X + 0.0221$.7979
Squared coefficients	$y_{\text{squared}} = -0.0285X - 0.1071$.8475
Linear coefficients	$y_{\text{linear}} = 0.2911X + 4.9979$.8388
Constant term	$y_{\text{constant}} = -3.6437X + 37.423$.8938

*y = either the cubic, squared, or linear coefficients or the constant terms from the 5 polynomial equations and X = median age at death of mixed breed dogs in the 5 weight categories.