

LONGEVITY AND MORTALITY OF IRISH WOLFHOOUNDS

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(With 2 figures in the text)

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INTRODUCTION

Evidence of the relation between age and force of mortality from birth to senescence is available for very few vertebrates. While life tables exist for man, the laboratory rat and mouse, and several small rodents (*Microtus* : Leslie & Ranson, 1940, Leslie, Tener, Vizoso & Chitty, 1955 ; *Mastomys* : Oliff, 1935) there are only partial data for any of the larger mammals (horses: Schiermann, 1948; ewes: Carter, 1939, Kelley, 1939). The most needed data of this kind for comparative studies of senescence are those dealing with birds and poikilothermal vertebrates, but it is also desirable to extend the number of mammals whose pattern of ageing and mortality is known. This is extremely difficult. Of large mammals kept under observation and record throughout life only horses, domestic pets, and zoological garden specimens are commonly allowed to reach old age, and large selective biases exist in the records of their longevity.

For comparative studies we ideally require the dates of birth and death of a large number of unselected individuals, living under uniform conditions which permit them to reach old age, and not exposed to loss from sale, culling, or other kinds of interference with the validity of the sample. This is a counsel of perfection, and in view of the scarcity of data any record which enables us to estimate the relation between age and mortality in a large number of animals of the same species and breed is of interest.

Data of this kind certainly exist for dogs, but are hard to find. Incompleteness, and loss of many adult dogs from the record by sale, make most kennel books disappointing as sources of information on adult longevity.

This paper deals with information obtained from a kennel book of Irish wolfhounds kept, and kindly abstracted for us in detail, by Miss D. Gardner,

of Curraclloe, Eire. The information is unusually complete in that while most of the dogs were sold, contact was maintained with the buyers, and the fate of most of the animals ascertained and entered in the kennel book. It is also of interest in giving a curve of survival for one of the largest breeds of dog which is not at the same time acromegalic.

MATERIAL

The kennel book recorded the births of wolfhounds between 1927 and 1945. There were entries of the birth of 189 animals, ninety-four dogs and ninety-five bitches. From these entries it was possible to find:

(1) the exact dates of birth and death of all the animals born alive and dying within the first twelve months of life, a total of thirty-six dogs and twenty-seven bitches,

(2) the exact dates of birth and death of seventeen dogs and twenty-three bitches which died after the first year of life,

(3) the exact date of birth and the year of death of a further twenty-six dogs and twenty-five bitches.

We have therefore a record of the exact life-span of 103 animals, and of the life span to the nearest year of 154.

In dealing with these entries, "natural death" was arbitrarily taken to include deaths from illness, poisoning, or whelping, and animals destroyed by reason of disease, but to exclude accident and animals destroyed by reason of injury or vice. No stillbirths are included in the record, though they must have occurred. The figures for group (1), group (2), and groups (2) and (3) combined, have been treated separately. Group (1) is a complete record, from which were calculated the infant (up to one month) and juvenile (up to one year) survival and mortality, accidental deaths being included in the usual way. Groups (2), and (2) plus (3), were computed separately to see how far the ages for the whole sample agreed with those of the accurately-known portion of it. A short life table was then based on the number of animals, alive at a working origin $x=1$ year, whose subsequent death was recorded, excluding those known to have died of accidental causes, by yearly intervals. This table is incomplete compared with the real population at its starting-point, fifteen dogs and twenty bitches being lost to the record at unascertainable ages. The positions of known accidental deaths are marked on the table, but not included in the computation.

RESULTS

The sex ratio at birth for all recorded births, ninety-four males and ninety-five females, was 99. Stillbirths were not entered in the kennel book. There were twenty-five litters containing more than one live puppy (range 2 to 12, mean 6.6) and these produced eighty-six dogs and seventy-nine bitches, a sex ratio of 10:9.

The probability at birth of reaching the age of one month was 0.7447 for dogs and 0.8842 for bitches (mortalities 0.2553 and 0.1158) and the corresponding probabilities of reaching one year were 0.6129 and 0.7292.

TABLE 1

Mean and median lifespans of wolfhounds reaching one year of age whose exact dates were known (Group 2) and of all wolfhounds reaching one year of age whose year of death was known (Groups 2 & 3)

	n	$\bar{x} \pm 2\left(\frac{s}{\sqrt{n}}\right)$	Standard devn.	Median
<i>Group (2)</i>				
(months)				
Males	15	61.77 ± 19.8	38.34	36
Females	20	83.05 ± 21.3	47.54	97
<i>Groups (2) & (3)</i>				
(years)				
Males	39	4.95 ± 0.94	3.00	3.6
Females	44	6.59 ± 0.95	3.15	6.6

TABLE 2

Life table for Irish wolfhounds in the first year of life (radix 94 males, 95 females at birth) and in subsequent years by annual groups (radix 39 males, 44 females alive at one year)

Age (x)	MALES				x	FEMALES			
	No. of deaths		l _x	q _x		No. of deaths		l _x	q _x
	d _x	a _x				d _x	a _x		
0-1 months	24		1.0000	0.2553		11	1.0000	0.1158	
0-1 years	34	(2)	1.0000	0.3871		26	(1) 1.0000	0.2708	
			0.6129				0.7292		
Years									
1	6		1.0000	0.1538	3.76	4 (1)	1.0000	0.0909	5.59
2	12	(2)	0.8462	0.3636	3.66	4 (1)	0.9091	0.1000	5.10
3	3		0.5385	0.1429	4.04	2 (1)	0.8182	0.0556	4.61
4	1	(2)	0.4615	0.0556	3.61	2	0.7727	0.0588	3.85
5	3		0.4359	0.1763	2.76	7	0.7273	0.2188	3.06
6	2		0.3588	0.1429	2.28	6	0.5682	0.2400	2.78
7	6		0.3077	0.5000	1.58	3	0.4319	0.1579	2.50
8	2		0.1538	0.3333	1.66	6	0.3636	0.3720	1.88
9	1		0.1026	0.2500	1.24	6	0.2272	0.6000	1.70
10	3		0.0739	1.0	0.50	1	0.0909	0.2500	2.50
11			0.0			0	0.0682	0.0000	2.16
12						1	0.0682	0.3333	1.17
13						2	0.0455	1.0	0.25
14							0.0		
n= 39 (4)					n=44 (4)				

l_x = number of individuals alive at time x (radix 1.000)

d_x = number of observed deaths from "natural causes" between x and x + 1.

a_x = number of observed deaths from "accident or violence" between x and x + 1.

q_x = rate of mortality for the period x to x + 1.

e_x = expectation of life in years of an individual alive at time x.

Accidental deaths are considered in calculating mortality from 0-1 year, but excluded from the calculation for subsequent years.

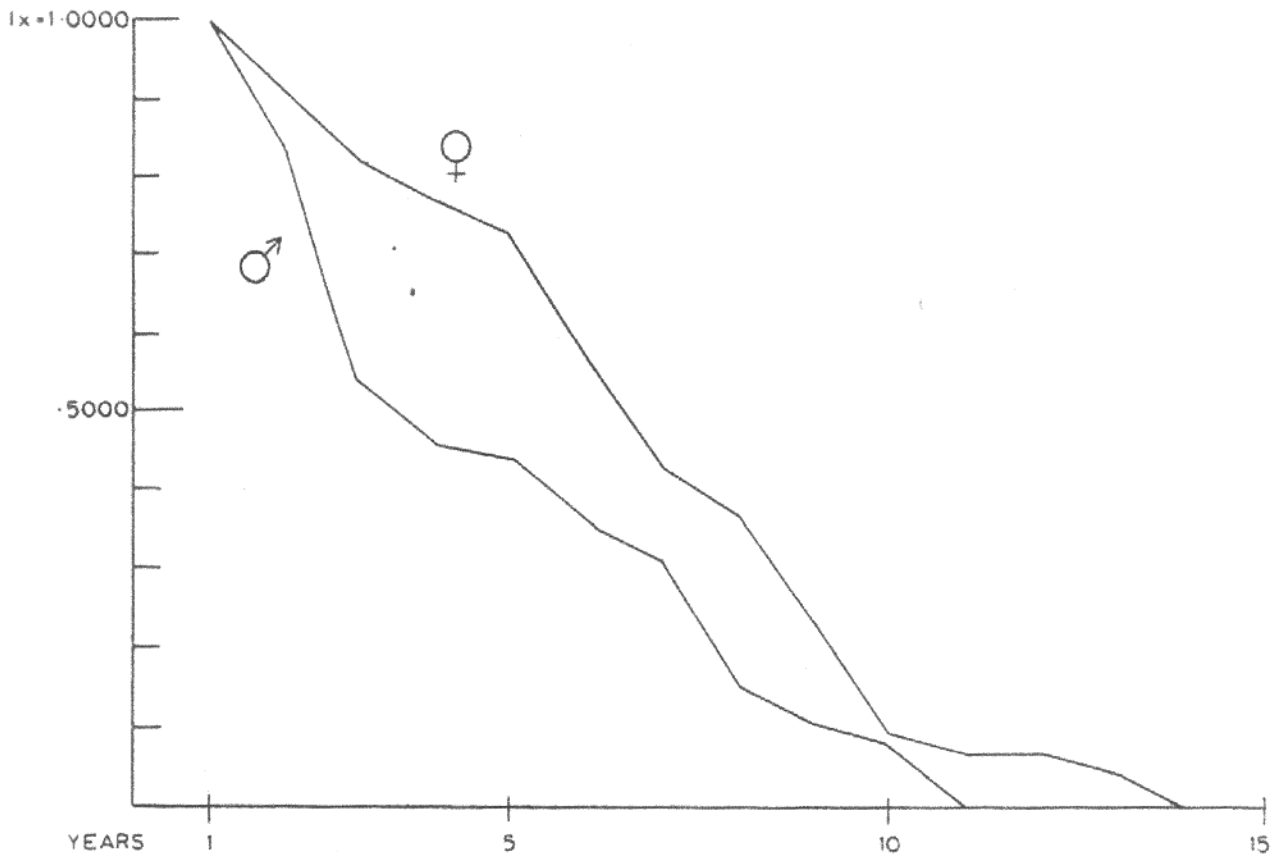


Fig. 1.—Irish Wolfhounds: survival curve of thirty-nine dogs and forty-four bitches from one year of age—annual totals.

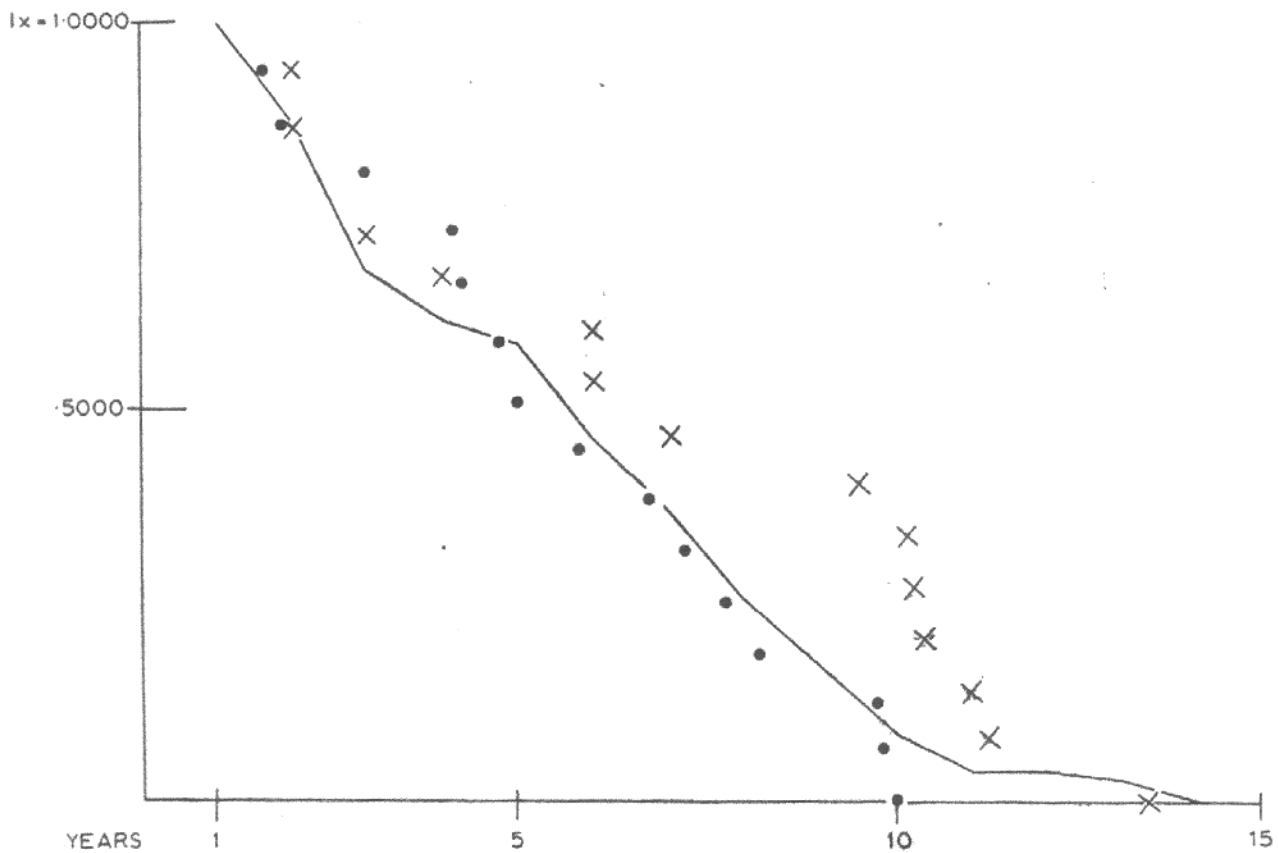


Fig. 2.—Survival curve of thirty-nine male and forty-four female Irish wolfhounds from one year of age (sexes combined). The superimposed points represent ages at death of fifteen spaniels from the same kennels (+--++) and fifteen dingoes bred in the London Zoo (●-●-●).

The maximum ages recorded for each sex occurred in animals whose exact dates were known - dog, 126 months (29/8/1935 to 9/2/1946), bitch 161 months (4/2/1940 to 13/7/1953).

We calculated the mean and median life-span in months of animals in group (2), and the mean life-span and median year of death for groups (2) and (3) combined. These form Table 1. A Life-table based on the unsmoothed data for groups (2) and (3) is given in Table 2 and the corresponding survival curves in figs. 1 & 2.

DISCUSSION

The tables and survival curves based on this material show (1) a sex difference in mortality at all ages in favour of the female, which is in the usual direction but is unusually large, (2) a curve of survivorship for the combined sexes which is nearly linear on an arithmetic scale over the greater part of adult life. A curve of this shape indicates that although the rate of mortality increases with age, it does so at such a rate that roughly the same number of individuals die in each year. A high variance in age at death might be expected in an inbred line if death is not due to a single characteristic cause, since the variance of many characters associated with vigour tends to increase with increasing homozygosity, but the same sort of curve is also found for the combined sexes in several populations of random-bred mammals which we have studied (sheep, cavies (*Dolichotis patagonica*)) and which were kept in zoological gardens, probably under suboptimal conditions (Comfort, 1955 b).

We have not yet found actuarial data for other breeds with which these can be compared, apart from studies of mortality in puppies (Druckseis, 1935). The voluminous study by Stockard (1941) of breed and constitution makes no mention of the life-span. But the longevity of dogs, judging from maximum age records, appears to be lowest in large and inbred as against small and inbred or small and random-bred strains, size being probably the higher scoring factor, since we have very long records (nineteen years) in pure-bred Pekingese. The Irish wolfhound is one of the largest breeds, individuals reaching 100 kg (Stockard, 1941), compared with 1 kg in the Chihuahua and from 3 to 4 kg in the Pekingese. It is, however, skeletally well-proportioned and is not known to be subject to any endocrine abnormality.

One reason for the short life of large dogs is perhaps the relation between size and tumour incidence (Cotchin, 1954) which is higher in some of the largest, and strikingly low in small breeds, such as the Pekingese. Physical disproportion probably plays a part, however, in increasing the vulnerability of large individuals to cardiac or respiratory disease. This effect of gigantism has long been recognised in man.

Flower (1931) estimated that for dogs kept as pets under domestic conditions the mean life-span was probably well under four years. The upper limit for all breeds lies somewhere in the region of twenty years, ages over sixteen being very uncommon, and higher ages (thirty-seven years, Lankester, 1870) being undocumented. This is in striking contrast to the longevity of cats, which can undoubtedly reach or even exceed twenty-eight years (Mellen, 1940; Comfort, 1955 a).

Sex differences in mortality

Although in these figures the infant mortality of dogs is significantly higher, and the expectation of life at all ages lower, than those of bitches, the large sex difference in mean longevity is mainly due to high mortality of dogs in the second and third years of life. This may well represent a real difference, in spite of the smallness of the samples. In early adult life the number of animals withdrawn from the record must increase progressively, but since dogs are of greater sale value to breeders (Druckseis, 1935) and more bitches than dogs are kept in a breeding stock, dogs dying young are more likely to have been omitted through sale and lack of record than bitches at the same age.

Lower viability in males is probably general in mammals, the exceptions being due to special conditions, genetic or environmental (*Mastomys*: Oliff, 1953) although it is not uncommon for the oldest recorded individuals to be males, and the male variance is normally the greater. The same is probably true not only for forms where the male is heterogametic, but also for birds (Pease, 1947) and some at least of the Lepidoptera: the literature of this question is reviewed elsewhere (Comfort, 1955 b). The relative contributions of "maleness" and homozygy to this bias are still in dispute - both probably contribute in heterogametic males, while one effect of inbreeding may be to produce marked differential mortality between the sexes, though not always in favour of the female (Clarke & Maynard Smith, 1955).

In these wolfhounds the difference is in the usual direction, but its distribution is peculiar, and suggests that dogs are either more susceptible to infectious disease during young adulthood than bitches, or more easily killed by it, especially during their second and third years of life. There was no comparable mortality in young bitches, and the deaths were well spread through the record over a number of years: they did not represent a single epizootic. Of twelve dogs which died in their third year, four did so from distemper, four of "gastroenteritis", two of pneumonic infections and one of unstated causes, while one was destroyed as a result of persistent fits.

The causes of death recorded in old animals likewise differ between the sexes. Of the four oldest dogs, dying in their tenth year, three are said to have had "heart disease", whereas all the three oldest bitches, one in her fourteenth and two in their thirteenth year, died or were destroyed following mammary carcinoma, and another in her ninth year died after an operation for uterine tumours. No tumours were recorded in any of the dogs.

Longevity and inbreeding

. Inbreeding may adversely affect the life span either through inbreeding depression per se, or through selection of a deleterious factor (cancer susceptibility, pigeon-chestedness), or both. The breed discussed here is of long standing and has probably reached a stable life-span not susceptible to further depression under present conditions of crossing. This state of affairs is common even in strictly-inbred laboratory strains: thus in *Drosophila* "within an even moderately inbred line the genetic differences in duration of life remain constant over periods of at least ten to fifteen, or more, generations" (Pearl & Parker, 1922) and may be little altered even by selection for longevity (Comfort,

1953). In such strains the life-span can be strikingly increased by out-crossing. Clarke & Maynard Smith (1955) found that hybridization between such strains of *Drosophila* doubled the imaginal life-span, and caused the curve of survivorship to move bodily away from the origin without significant change in slope - in other words, the additional life-span represented a period of very low mortality interposed before the onset of the senile decline. The longer life-span of the hybrids was found in this case to be closely similar to that of wild-caught flies.

Heterosis can certainly produce effects of similar magnitude in mammals (Gates, 1926): in general the limit of longevity in the presence of hybrid vigour is probably close to that which would be shown by a hypothetical "wild" strain under good conditions. Comparisons drawn from real wild mammals in captivity ignore the adaptation of domestic animals by selection for vigour under domestic conditions. It is interesting, however, to compare the life-span of wolfhounds with some isolated data for another breed in the same kennels, and for a series of fifteen dingoes (*Canis familiaris dingo*) bred in the London Zoo. In Fig. 2 the ages at death of fifteen spaniels (field and crossbred) from Curracloe and of the dingoes are superimposed on the survival curve of the combined wolfhound sexes. The greater life-span of the spaniels is not statistically significant in view of the small and selected sample, but is in the expected direction, since field spaniels may live for eighteen years (Flower, 1931). The fit between the survival curve of wolfhounds and the ages of death of the "wild-type" dogs is fairly close. Bearing in mind that the life of zoo specimens may be unpredictably longer or shorter for environmental reasons than that of domestic pets, and that they may show depression due to several generations of inbreeding which is not yet stabilized, it seems that the life of wolfhounds has at least not been greatly curtailed either by loss of vigour or by the effects of size.

This is borne out to some degree by the limited data which exist for related species, many of which reach a limiting age between eleven and fifteen years (jackals, coyotes, Flower, 1931; ranch bred foxes, Sheldon, 1949). According to Flower, thirty adult wolves dyeing in the London zoo had a mean age of nine and a maximum of thirteen and a half years, though sixteen years is recorded. The difference in longevity between wolfhounds and wild canines is substantially less, on these data, than that between most inbred lines of laboratory mice and the F_1 progeny of wild-caught mice and voles in captivity.

SUMMARY

1. Life tables and survival curves have been constructed from kennel records of 189 Irish wolfhounds.
2. The maximum recorded ages in months were males 126, females 161, and the mean ages at death of animals surviving to one year were: males 4.95 ± 0.94 years and females 6.59 ± 0.95 years.
3. The viability of bitches was higher at all ages than that of dogs. There was a particularly heavy mortality of dogs in the third year of life.
4. The influence of large size and of inbreeding depression on the longevity of the breed is discussed.

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