ASPECTS OF THE BIOLOGY OF SUBURBAN FOXES

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ABSTRACT

The occurrence of wild canids living in close association with man is documented, and it is seen that foxes living in suburbia are a unique British phenomenon. Foxes have lived in London for at least 35 years, and have now permanently colonised most suitable habitats.

The various body measurements of suburban foxes are compared with similar data for other populations. It is shown that the tail is shorter than in populations from regions with colder winters, the other body measurements varying from one population to another but with no obvious pattern.

Various age determination techniques have been applied to the Red fox, but for the majority of techniques separation of year classes is impossible after eighteen months of age. The only technique that has proved of value is the use of incremental lines in the tooth cementum, particularly in the premolar teeth of the lower jaw.

Growth curves have been constructed for animals up to six years of age.

Using the age of the animals as determined by cementum lines, a life table for suburban foxes has been constructed. These data are used to compare the structure of the suburban fox population (subject to limited control operations) with that of a fox population subject to intense control. Survival curves have been constructed. It is shown that only the ratio of young : adults is affected by intense control operations, and that the rate of adult mortality is identical in both populations. The significance of this is discussed in relation to rabies and sarcoptic mange.

The general health of the population is illustrated using spondylosis deformans as an example. This condition has not been reported previously in foxes.

The food habits of suburban foxes have been examined. The various techniques available have been evaluated, but only stomach contents and den litter proved of value in the present study. The results are discussed in relation both to other fox food studies and the prey species available in London.

The validity of the term "suburban fox" is considered, comparing the data presented here with similar data for other fox populations.

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PREFACE

This work was carried out between November 1971 and September 1974, while in receipt of a Natural Environment Research Council Postgraduate grant, which is gratefully acknowledged. The work was completed at Royal Holloway College, and my thanks are extended to Profs. P. Butler and P. Jewell for the facilities provided.

The carcasses used in the study were supplied by many individuals involved with fox control in London, and my thanks are due to Messrs. B. Brown, R. Clark, M. Clarke, J. Death, B. Gundy, J. Hayward, J. Hoad, R. Hogben, K. Hoy, R. Lawer, D. O'Connell, A. Roberts, A. Sales, N. Vessey and R. Vessey. I would also like to acknowledge the support received from the Chief Public Health Inspectors (Chief Environmental Health Officers) of the London Boroughs of Barnet, Bexley, Bromley, Croydon, Greenwich, Harrow, Hillingdon, Lewisham, Merton and Sutton, and the Chief Public Health Inspectors of Epsom & Ewell and Esher District Councils.

The photographs were produced by Messrs. M. Colthorpe and S. Horrell, and for the identification of the insect remains in the stomach contents I would like to acknowledge the assistance of Drs. R. Angus, V. Brown and J. Pontin.

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Apart from the assistance acknowledged, this thesis is my own unaided work and describes a previously unpublished study. A paper on syndactyly in foxes is appended in support of the thesis.

This thesis contributes to the knowledge of fox biology in a number of ways. It is the first study into the biology of suburban foxes, which are unique to British towns and cities. The efficiency of a variety of age determination techniques has been compared when applied to a single population. The age data so obtained have been used to determine the age structure of the suburban fox population, and the first lifetables for a Red fox population have been constructed. The occurrence of spondylosis deformans in the population has been described; this condition has not previously been reported in the Red fox. This is also one of the first studies of the course of development of a pathological condition in a wild mammal population. The food habits of suburban foxes are described, and the myths concerning their food habits dismissed.

SECTION 1
INTRODUCTION

The occurrence of wild animals in a suburban environment has, in recent years, become a topic of major interest to naturalists and conservationists and has been the subject of several books (e.g. Kieran 1959, Mabey 1973 and Burton 1974). Yet despite the general interest centred on suburban wildlife, and although there are good reasons to encourage ecological and behavioural studies of urban wildlife, Sinton (1970) noted that such research is seriously lacking.

One of the first suburban animals to be studied in detail was the Indian rhesus monkey (Macaca mulatta), which has shared cities with man for centuries. Singh (1969) compared monkeys living in their native forest habitat with those living in cities and showed that with the change in habitat there was also a change in various aspects of the animals' biology (group composition, diet, group leaders' behaviour and also in psychological complexity).

Some interest has focused recently on stray dog populations living in suburban areas, particularly in American cities. Carding (1969) noted that stray dogs have lived in close association with man for thousands of years, and that these populations have ranged from a few individuals present sporadically on the fringes of camps to the many thousands of animals living permanently in a large city. Carding also found that these animals are capable of causing a nuisance in a variety of ways, which included (a) spread of disease, (b) inflicting wounds on people, (c) damaging property, (d) creating a hazard on roads, and (e) excessive noise. It is interesting to note that, with the exception of the second point, suburban foxes create a nuisance in exactly the same ways. Beck (1973) made a detailed study of the stray dog population of Baltimore, a city of 72 square miles with a population of nearly one million people. He estimated a total free-ranging dog population of between 32,400 to 54,000 animals. Despite the very different nature of the populations under investigation, Beck's study and the present study found many ecological and biological similarities, and comparisons between the two studies will be made later in the thesis.

Although stray domestic canids have lived in close association with man for several thousands of years, wild canids only rarely enter suburban environments. The coyote (*Canis latrans*) lives in Los Angeles, where Froman (1961) noted that the animal was found even in the heart of the city, and in a few other western cities such as Houston, Denver and Boise where it was found on the outskirts of the city. Only in Los Angeles was the animal widely distributed, and several hundred individuals (including coyote-dog hybrids) were thought to be present. Of these, about twenty were caught each month in leg-traps. Here, however, the situation was not one of an animal invading suburbia, as occurred with the fox in London, but of an animal persisting as the suburbs expanded. Also, the coyotes were living in relatively rural habitats such as the beds of dry creeks, the sides of steep hills, and the edges of estates, habitats which did not bring the animals into very close contact with man.

The wolf (*Canis lupus*) will also enter towns and cities; this usually happens during the winter months in response to a shortage of food, and the animals do not stay long. The main accounts relate to the Old World, and many such events are documented by Pollard (1964). He recorded that a rabid wolf entered the town of Carmarthen in 1163 and bit 22 people, most of whom subsequently died. The suburbs of Paris were invaded by several wolves during the civil struggles after the Hundred Years War at the beginning of the fifteenth century, apparently to take advantage of the abundance of unburied corpses that littered the streets. Even more striking was the invasion of the village of Pilova by large numbers of wolves, this happening in Siberia as recently as 1927. Here the inhabitants were beseiged by the animals, and many people were attacked and killed before relief finally arrived.

In contrast, the occurrence of foxes in suburbia seems to be a unique British phenomenon, foxes now being found in most of the larger towns and cities; no similar ecological situation is seen even in nearby continental Europe. In Australia the introduced Red foxes are sometimes found on the outskirts of large cities; a recent newspaper report (Sunday Express 25-6-1972) described a "plague" of foxes on the outskirts of Melbourne, where they caused considerable damage to a cabbage crop, 1,000 cabbages being eaten on a 50-acre farm in one month. This is, however, a rare event, and even then the foxes were not living in a truly suburban environment.

In American cities, despite their more open nature, foxes are virtually non-existent, and their ecological niche is often filled by the raccoon (Procyon lotor). Jones (1958) compiled a list of American suburban pests, noting that most were left as remnants after the suburbs expanded. His list of common suburban pests was: bats, chipmunks, Flying squirrels, Grey squirrels, Ground squirrels, opossums, Pocket gophers, Cottontail rabbits, skunks, woodchucks, Meadow mice, Pine mice, White-footed mice and moles. Other species encountered as occasional pests in some areas included armadillos, badgers, beavers, deer, muskrats, porcupines and woodrats. Jones made no mention of foxes. Similarly MacMullan (1968) noted that 90% of the time of Michigan conservation officers in metropolitan areas was occupied by complaints of squirrels, raccoons, opossums, bats, rabbits, and even skunks, but again no mention was made of foxes.

Kieran (1959) described the wild life of New York City. He noted that it was illegal to hunt within the city limits and that as a result the raccoons led a protected and well-fed existence, being present in some numbers in the outlying sections of Queens and Bronx. Yet despite the absence of hunting pressures Kieran noted that foxes were comparatively rare, persisting only in the northerly section of the Bronx, where both Red foxes and Gray foxes (Urocyon cinereoargenteus) were found; this area is, however, very rural and consists of swamps and large natural parks. This situation seems to have persisted to the present day without change, Shoman (1970) noting that in Bronx Park, where much of the area is still in a natural state, a fox bark is occasionally heard. Shoman did list the fox as being one of a wide range of animals seen in Smoke Rise, a 3,500 acre New Jersey development where homes were blended into a natural setting, although this again is not a closed suburban habitat. That the situation seen in Britain is so totally different from that in America is exemplified by Shoman's statement that "outside of London, in Epping Forest, foxes roam at will"; Shoman expressed surprise that foxes could be found so close to a large city!

Teagle (1967) documented the invasion of the fox into the suburbs of London, and little further comment need be made on this account. Briefly, he noted that during the period 1930 to 1958 foxes were known from a number of localities, particularly Hampstead Heath, Middlesex, and that there was evidence in the 1940s that the animals were becoming commoner in suburban Surrey and Kent. During the period 1959 to 1965 Teagle collated all available records; in the early 1960s the fox could be found regularly within ten miles of the city centre at Blackheath, Walthamstow, Wimbledon and Norbury, with occasional animals even nearer the city centre. By the end of his survey Teagle found that on the Essex side of London foxes had penetrated as far as Barking, Leyton and Wanstead; in Kent foxes were found within six miles of St. Paul's Cathedral; in Surrey there were records as close to the centre of London as Streatham, Dulwich and Lambeth; in Middlesex the inner most limit of the breeding population still seemed to be Hampstead, although foxes were recorded as far into London as Hyde Park.

Teagle noted that the present situation was the result of invasion rather than through an increase in existing populations which had become isolated when the suburbs spread. Teagle also discussed the factors which may have initiated such an invasion, particularly the effects of hard winters and of myxomatosis, and he wisely concluded that these factors alone did not constitute a satisfactory explanation for such an invasion. The availability of bomb sites after the Second World War might also have been a contributary factor, underestimated by Teagle, since foxes are now reported to be increasing in number in Belfast as the direct result of the availability of bombed areas as harbourage.

Beames (1969, 1972) documented the further advance of foxes into suburban London. He noted that the fox appeared to have spread into the inner parts of the city and was regularly recorded from New Cross and Dulwich to the east to Wandsworth and Putney in the west; they were seen regularly in places such as Hammersmith, Kilburn, Highbury and Hackney. Beames also noted that it appeared that foxes had occupied most of the suitable areas containing open spaces and large gardens in the southern half of the area.

Occasional foxes turn up even nearer the centre of London. For instance on September 11 1972 a fox was run over in Blackfriars Underpass in the City of London itself (The Field 5-10-1972 and Horse and Hound 6-10-1972), and it was suggested that the animal was living in the bomb sites of nearby Temple Garden. Similarly, a fox was run over in York Road, Waterloo (within half a mile of Charing Cross) in February 1975 (The Sun 18-2-1975).

As can be seen from this brief resumé, foxes are now widespread throughout London. Breeding populations are found only a few miles from the centre of the city, and occasional animals occur even further in; they are still increasing in numbers and expanding their range slightly, yet these animals are the offspring of no more than 35 generations of suburban foxes. There has been some discussion as to which habitats in London are of importance to foxes, particularly as breeding sites and daytime harbourage. Beames (1969, 1972) noted that foxes had occupied most of the suitable areas containing open spaces and large gardens in the southern half of the area. However Beames was wrong in his assumption that parks and large gardens are of paramount importance to foxes. Open spaces are avoided by foxes as harbourage, since they are heavily populated during the day, and such areas are over-run by dogs being exercised; grassy lawns are, however, of importance in the early morning as sources of earthworms for the foxes (Section 7). That suburban foxes rarely use parks for lying-up during the day is confirmed by Simms (1974), who described the wildlife of London's Royal Parks. The only Royal Parks in which foxes are common are Richmond and Bushey, where large areas of land are inaccessible to both the public and their dogs.

Most fox earths, and daytime harbourages, are in quiet gardens, irrespective of their size, which may be either well kept or neglected and badly overgrown. Such gardens are usually owned by old people or immigrants, who neglect the garden, or by people without children and dogs. In such situations foxes are active throughout the day. Also of importance are London Transport and British Rail railway embankments, which are becoming more overgrown and impenetrable in the absence of regular burning.

The habitats in which suburban foxes are found render control operations either difficult or impossible. London Transport and British Rail Bye Laws prohibit the carrying or use of fire-arms on their properties, so that only gassing operations are allowed, and since adult foxes rarely use earths this means that only young cubs are destroyed by spring gassing; gassing at any other time of the year is pointless. On private property there is often a conflict of opinions, some people wanting their local Council to control foxes, while other people demand their preservation. If foxes are living in two or three neighbouring gardens they can often only be shot in one of the properties so that some of the animals escape. Similarly people often complain to their Council about fox damage but no action can be taken since the foxes are living in a neighbour's garden, where they are protected by the landowner. Such a conflict of opinions ensures the continued survival of foxes in the London suburbs.

Since no research has previously been conducted on suburban foxes any aspects of their biology, ecology or behaviour could have been studied. Time has permitted only a limited number of aspects to be studied, these being chosen to demonstrate the way of life, general health and adaptations of suburban foxes.

SECTION 2

COLLECTION OF MATERIAL

2.1 STUDY AREA

The study area was taken as the urban areas within the Greater London Boundaries; in some areas, particularly on the south-west and north-east sides of London, the built-up area has spread beyond the G. L. C. boundary, and foxes have been collected from these areas as well. In the early part of the study the supply of foxes from the suburban area was very erratic, and some foxes were collected from the fringes of London, particular the outlying suburbs of the Green Belt zone. These animals interchange with those living within the Greater London boundaries and form part of the same population.

2.2 SUPPLY OF MATERIAL

Most fox cadavers were obtained from the Borough Public Health Officers, the animals being killed in response to specific complaints. The methods of dealing with complaints vary (Table 1). Many animals, particularly litters of cubs, are killed by gassing and these corpses are not recovered. The London Borough of Sutton relies heavily on box-trapping to control its fox population and these animals could not therefore be used for stomach contents analysis. However, despite the problems of shooting in a built-up area, most Boroughs rely on this method of fox control and animals killed in this way formed the bulk of the sample.

In one or two areas private individuals undertook fox control work. A large sample of animals (20 in all) was obtained from an individual

TABLE 1

SIZE OF THE 33 GREATER LONDON BOROUGHS AND THE FOX CONTROL MEASURES IN OPERATION (ACREAGE GEBBETT 1972).

Borough	Total Acreage	Open Spaces (acres)	Residential (acres)	Fox Control Measures In Operation
Barking	8, 877	1, 324	2, 666	No fox problem.
Barnet	23, 124	7, 391	8, 116	Occasional foxes shot in response to specific complaints.
Bexley	15, 896	4, 240	5, 530	Large number of foxes shot annually by the Council.
Brent	10, 923	1, 496	4, 826	No fox problem.
Bromley	39, 293	20, 834	10, 907	Large number of foxes shot or gassed annually in the built-up area.
Camden	5, 365	1, 043	1, 923	No fox control at present.
City of London	739	22	8	No fox problem.
City of Westminster	5, 464	1, 109	1, 297	No fox problem.
Croydon	23, 812	3, 018	8, 950	Foxes controlled mainly by gassing; some shooting and trapping.
Ealing	13, 708	2, 892	5, 032	No fox control.
Enfield	20, 060	7, 532	5, 931	Foxes shot very occasionally.
Greenwich	12, 565	2, 636	3, 984	Foxes controlled by shooting carried out under contract.

Borough	Total Acreage	Open Spaces (acres)	Residential (acres)	Fox Control Measures In Operation
Hackney	4, 815	769	1, 898	No fox control programme.
Hammersmith	4, 181	538	1, 421	No fox problem.
Haringey	7, 490	1, 299	3, 044	Very few foxes present and no control necessary.
Harrow	12, 555	2, 956	5, 825	No control carried out by Council; some foxes shot by private individual.
Havering	29, 650	13, 412	6, 768	Foxes common but no control operations during study period.
Hillingdon	27, 259	9, 981	6, 499	Foxes controlled by regular shooting by Council; some box-trapping.
Hounslow	14, 631	3, 482	4, 040	Foxes rare - only a few are shot.
Islington	3, 679	117	1, 564	No fox problem.
Kensington and Chelsea	3, 015	381	1, 223	No fox problem.
Kingston upon Thames	9, 279	2, 680	3, 751	Foxes present but no fox control operations.
Lambeth	6, 840	681	3, 292	No fox problem.
Lewisham	8, 611	1, 171	4, 194	Foxes common and controlled by Council shoots and by contract shooting.
Merton	9, 379	2, 571	3, 570	Foxes controlled by occasional contract shooting.
Newham	9, 575	1, 077	2, 444	Foxes very rare - no fox control programme.

Borough	Total Acreage	Open Spaces (acres)	Residential (acres)	Fox Control Measures In Operation
Redbridge	13, 954	4, 411	5, 230	Occasional foxes - no fox control programme.
Richmond upon Thames	13, 967	6, 110	3, 757	Foxes common but no fox control programme.
Southwark	7, 374	896	2, 623	No fox problem.
Sutton	10, 729	2, 154	4, 817	Large number of foxes - controlled by box-trapping and some shooting.
Tower Hamlets	5, 322	356	1, 180	No fox problem.
Waltham Forest	9, 804	2, 200	3, 481	Only rarely troubled by foxes - no control programme.
Wandsworth	8, 860	1, 896	3, 467	Foxes rare - no fox control programme.
G. L. C. Owned Land	-	-	-	No regular fox control operations.
Total acreage in Greater London	399, 795	117, 675	133, 308	

in Barnet, who snared foxes in his garden in order to protect his wildfowl collection, and a few animals were also snared in Buckhurst Hill for the same reason. The main sources of material are shown in Table 2.

2.3 SEX RATIO OF SAMPLE

With the exception of one month, all the cub samples showed a preponderance of male animals, and for the total cub sample the sex ratio is 126 males : 100 females. This is due to two factors:-

a) male animals are more adventurous, and so more readily bolted by terriers. Females are less bold and are more often killed underground, their corpses never being recovered.

b) in many species of canids there is a real preponderance of male cubs. Johansson (1938), in a study of Swedish Silver fox farms, found that the sex ratio of cubs one or two weeks after birth, expressed as percentage of males, was 52.93 (112 males : 100 females). For three separate years, Layne & McKeon (1956) found that the sex ratio for Red fox foetuses collected in New York state was 147.4, 156.8 and 153.6 males : 100 females and for cubs the sex ratio for the same years was 102.7, 85.6 and 94.2 males : 100 females. Lund (1959) quoted the Norwegian Statistical Bureau of 1948, which noted that on 1-9-1946 there were 65,753 female and 71,768 male cubs among the Silver foxes on Norwegian fox farms, a sex ratio of 109.3. Fairley (1970) found that in Northern Ireland the sex ratio for embryos was 100 males : 96 females, and for juveniles the sex ratio was 100 males : 91 females.

The overall sex ratio for the cub sample is higher than that found in most studies, and this is attributed to a combination of a real preponderance of male cubs, and to the greater chance of recovering male cubs' corpses.

TABLE 2
SOURCES OF CADAVERS

Locality	Dogs	Vixens	Cubs		Total
			Dogs	Vixens	
Barnet, L.B. of	13	8	-	-	21
Bexley, L.B. of	10	7	-	2	19
Bromley, L.B. of	34	34	27	15	110
Croydon, L.B. of	2	7	-	-	9
Epsom and Ewell, U.D. of	-	1	-	-	1
Esher, U.D of	4	1	-	-	5
Essex Suburbs	16	16	4	1	37
Greenwich, L.B. of	6	9	10	11	36
Harrow, L.B. of	2	3	-	-	5
Hillingdon, L.B. of	19	11	11	7	48
Kent Suburbs	12	25	2	4	43
Lewisham, L.B. of	-	1	-	-	1
Merton, L.B. of	2	1	3	2	8
Redbridge, L.B. of	-	1	-	-	1
Richmond upon Thames, L.B. of	3	5	3	2	13
Surrey Suburbs	12	10	2	3	27
Sutton, L.B. of	2	7	5	6	20
Totals	137	147	67	53	404

TABLE 3

DISTRIBUTION OF CADAVERS THROUGH THE YEAR

	Dogs	Vixens	Cubs		Total
			Dogs	Vixens	
January	20	14			34
February	28	25			53
March	19	18			37
April	10	18			28
May	8	17	26	14	65
June	3	8	15	19	45
July	2	4	7	5	18
August	5	4	11	10	30
September	6	4	8	5	23
October	3	8			11
November	20	15			35
December	13	12			25
	137	147	67	53	404

The overall sex ratio for the adult sample was 93 males : 100 females, with a preponderance of males during the winter, and of females during the summer when most control operations are directed towards vixens and their litters. Layne & McKeon (1956) suggested that there may be a differential mortality during gestation or before the cubs left the den, so favouring the survival of females, and this differential survival may account for the decline in the proportion of males in the adult sample.

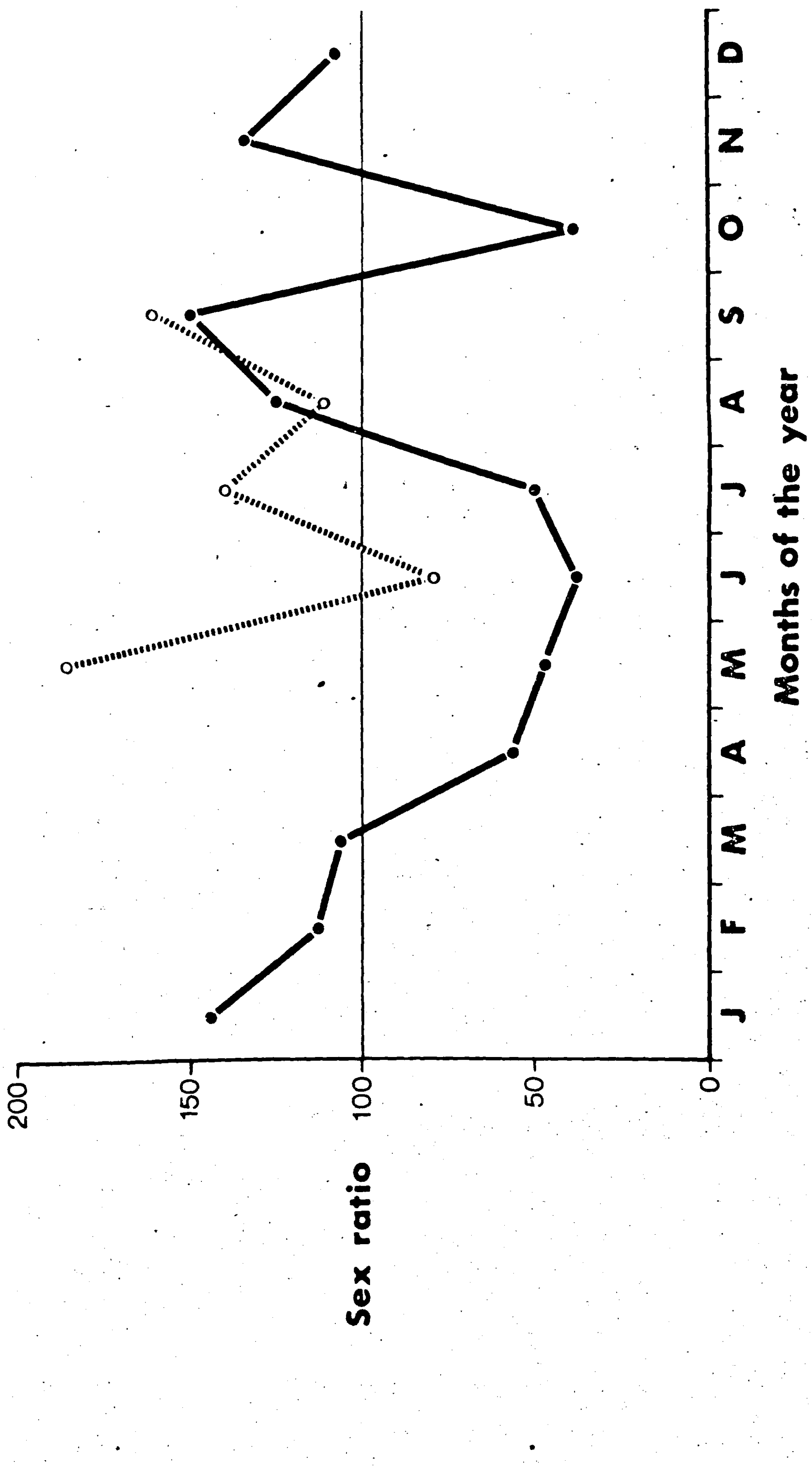
A similar annual variation in the sex ratio in the adult sample is confirmed by most workers, e.g. Lund (1959), but normally the overall sex ratio shows a preponderance of dog foxes in the total sample. Lund (1959) found an overall sex ratio of 123 males : 100 females and Fairley (1970) found a ratio of 100 males : 91 females. Layne & McKeon (1956), studying both Red and Gray foxes in New York, noted that in both species adult males outnumbered adult females throughout the year. However, the different sex ratios are an expression of different sampling techniques - Layne & McKeon obtained their sample from professional trappers who used foot-traps, and since dog foxes range more widely than vixens (e.g. Fairley 1969 a, Phillips, et al 1972, Jensen 1973) more dog foxes will be caught. The same applies to samples that include a large number of snared animals.

In London, however, very few animals are caught in this manner, and presumably organised shooting gives a fairer representation of the true sex ratio (although during peak birth periods shooting selects dogs and barren vixens, while animals near to parturition are underground). Thus McIntosh (1963a), studying foxes shot at night in the Canberra district of Australia, found a sex ratio of 53.3 males : 46.7 females (114 : 100) which did not depart significantly from an even ratio.

FIGURE 1 ANNUAL VARIATION IN THE SEX RATIO (NUMBER OF DOGS PER HUNDRED VIXENS) OF THE SAMPLE

●━━━━━━━━━● ADULTS

○┅┅┅┅┅┅┅┅┅○ CUBS


Sex ratio
200
150
100
50
0
J
F
M
A
M
J
J
A
S
O
N
D
Months of the year

SECTION 3
BODY SIZE OF SUBURBAN FOXES

3.1 INTRODUCTION

The size of foxes is often utilised as a character of importance in the recognition of subspecific or racial differences. Miller (1912) noted that Vulpes vulpes crucigera Bechstein from central and southern Europe has a maximum size rather less than that of Vulpes vulpes vulpes Linnaeus from the Scandinavian Peninsula. Tetley (1941) compared Scottish and Scandinavian foxes, and considered that they both belonged to Vulpes vulpes vulpes, and that these animals were distinctly larger than those found in central England. Similarly Hattingh (1956) compared foxes from Scotland and England. He found that there were no differences between foxes from Westmorland and southern England, and that the foxes from Scotland were of a distinct race.

Kolb & Hewson (1974) examined the body size of Scottish foxes collected from north-east Scotland and Argyll. These were compared with samples from England (Hattingh 1956), Norway (Lund 1959) and from Northern Ireland (Fairley 1970). Kolb & Hewson concluded that "too much stress has been laid on the similarity in size of Scottish and Scandinavian foxes" and that "each population of foxes probably has its own size characteristics which will have been evolved to suit certain ecological requirements, rather than there being a small number of distinct racial types".

3.2 RECORDING OF DATA

All undamaged carcasses were weighed, both entire and eviscerated, to the nearest ten grammes. The standard measurements of head plus body and tail lengths were recorded (±2 mm). The pinna, hind foot, length of the head from the tip of the nose to the external occipital protuberance, and the width of the head between the bases of the pinnae were also measured (±1 mm). The last two measurements were taken along the curvature of the head.

3.3 BODY MEASUREMENTS

The measurements of head plus body and tail length for 54 dogs and 46 vixens killed during the winter (October - March) were analysed in the same way as that used by Kolb & Hewson (1974), and for these measurements the range, means and standard deviations are shown in Figure 2, where the body size of suburban foxes is compared with samples from England, Northern Ireland, Norway and Scotland. The mean head plus body length for dog foxes from suburban London was larger than the same measurement for the other populations, with the exception of the Northern Ireland population, which had a slightly larger mean length. For the vixens the mean length was almost exactly the same as that for Scottish vixens, and these two populations formed the largest samples.

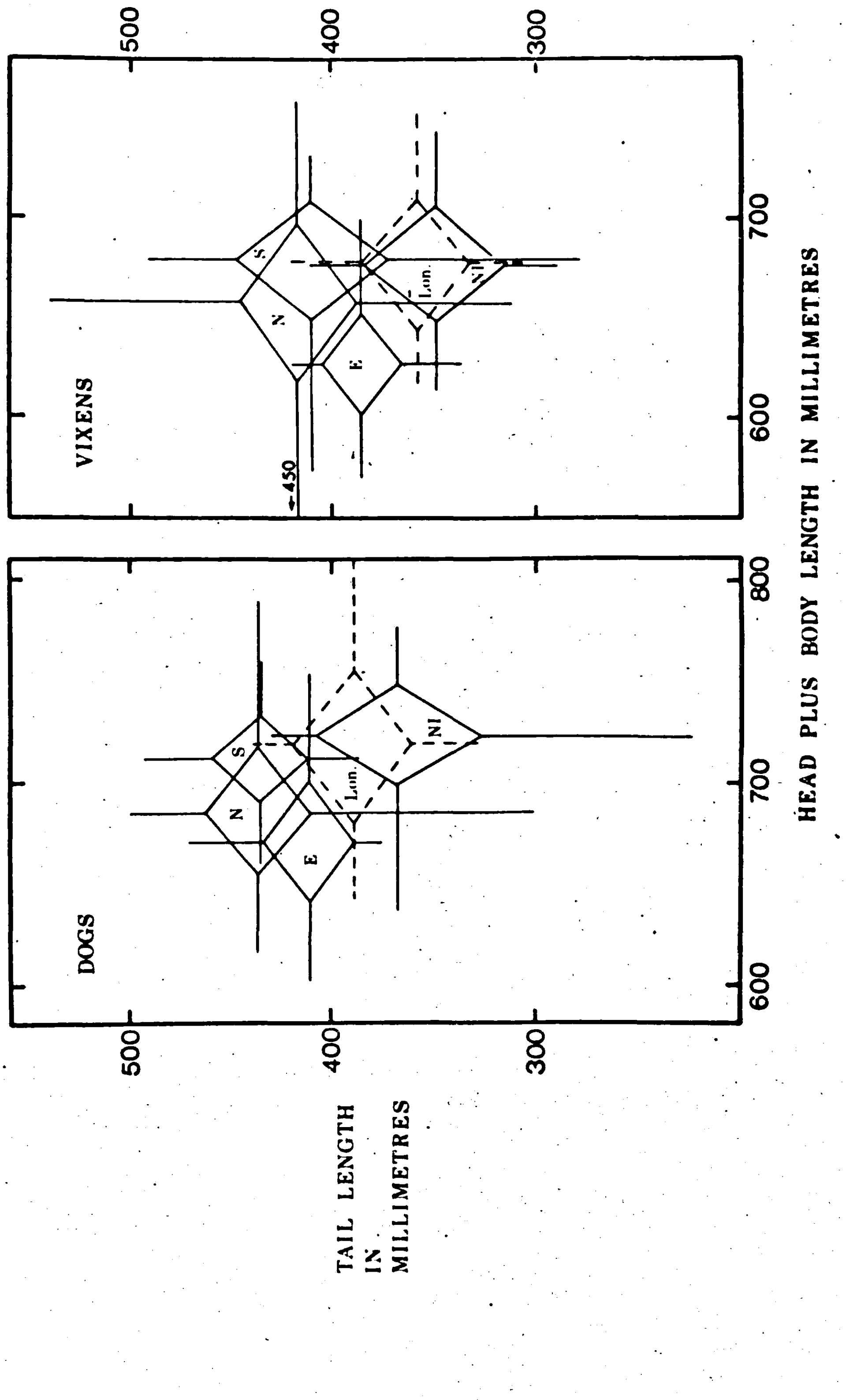
The most interesting point is the very short tail length seen in suburban foxes, and in both dogs and vixens the mean tail length is shorter than that from the other populations, with the exception of the sample from Northern Ireland. The samples show a distinct correlation between winter temperature and tail length, the short-tailed animals living in areas with a mild winter climate, such as Northern Ireland and suburban London.

Haltenorth & Roth (1968) quote Bergmann's rule that the size and weight of an animal increases from warm to cold areas, and they noted that

FIGURE 2 BODY SIZE IN FIVE FOX POPULATIONS, SHOWING THE MEANS, STANDARD DEVIATIONS (LOZENGES) AND RANGES (LINES)

E = ENGLAND
Lon. = LONDON
N = NORWAY
NI = NORTHERN IRELAND
S = SCOTLAND

BASED ON KOLB & HEWSON (1974).


DOGS
VIXENS
S
N
E
Lon.
NI
←450
500
400
300
600
700
800
TAIL LENGTH
IN
MILLIMETRES
HEAD PLUS BODY LENGTH IN MILLIMETRES

foxes from north-east Germany were larger than those from the south-west. However a simple explanation such as Bergmann's rule does not apply to fox body size data. As can be seen from Table 4, the greatest head and body lengths occur in populations from the mildest climates, but this increased size is counteracted by a reduced tail length, so that populations from milder climates are in total length shorter than most (but not all) populations from more rigorous climates. Hattingh (1956) could find no difference in the body size of foxes from southern England and Westmorland, despite the very different climatic conditions.

Comparing the other body measurements of hind foot length and pinna length (Tables 5 and 6), no distinct patterns emerge. The shortest ears are not seen in animals from the coldest areas, as usually attested. Neither do the largest animals have the largest pinnae and hind feet.

3.4 BODY WEIGHT

Body weight is affected by a number of factors. Lund (1959) showed that the body weight fluctuates with the season, dogs being heaviest in July/August and November, whereas vixens were heaviest in April (due to pregancy) and October/November. Similarly body weight is reduced by disease - sarcoptic mange reduces body weight by up to half that of the healthy animal.

To compare the body weight of suburban foxes only healthy, non-pregnant, winter-killed animals were used. 54 dog foxes were found to have an average weight of 6.43 kg.(range 5.16 - 8.20 kg) and 46 vixens an average of 5.45 kg.(range 4.00 - 6.77 kg.).

As can be seen from Table 7, the lightest foxes are those from Kansas. The American Red fox (considered to be con-specific with the Eurasian animals by Churcher (1959)) is consistently reported to be a small animal throughout its range. Rue (1969) recorded that the American

TABLE 4

COMPARISON OF BODY MEASUREMENTS FROM DIFFERENT FOX POPULATIONS.
ALL FIGURES ARE MEAN MEASUREMENTS IN MILLIMETRES.

Source of Material	Dogs			Vixens			Author
	Head and Body	Tail	Total	Head and Body	Tail	Total	
England	671	412	1083	627	385	1012	Hattingh 1956, re-analysed by Kolb & Hewson 1974.
Northern Ireland	723	367	1090	677	348	1025	Fairley 1970.
Netherlands	-	-	1101	-	-	1048	Haaften 1970.
London	719	389	1108	678	358	1036	Present study.
Norway	681	437	1118	663	418	1081	Lund 1959.
Scotland	712	436	1148	679	411	1090	Kolb & Hewson 1974.

TABLE 5

COMPARISON OF HIND FOOT LENGTHS FROM DIFFERENT FOX POPULATIONS. ALL FIGURES ARE MEASUREMENTS IN MILLIMETRES.

Source of Material	Dogs		Vixens		Author
	Range	Av	Range	Av	
England	135 - 170	152	125 - 150	141	Hattingh 1956
London	140 - 173	155	128 - 161	143	Present study.
Northern Ireland	109 - 173	161	134 - 166	151	Fairley 1970
Scotland	143 - 178	167	143 - 168	159	Kolb & Hewson 1974

TABLE 6

COMPARISON OF PINNA LENGTH FROM DIFFERENT FOX POPULATIONS. ALL FIGURES ARE MEASUREMENTS IN MILLIMETRES.

Source of Material	Dogs		Vixens		Author
	Range	Av	Range	Av	
London	82 - 102	93	78 - 99	89	Present study.
England	85 - 100	93	80 - 95	89	Hattingh 1956.
Scotland	87 - 106	96	85 - 100	93	Kolb & Hewson 1974
Northern Ireland	94 - 113	104	56 - 110	99	Fairley 1970.

fox weighs 8 - 11 lbs (3.63 - 4.99 kg.) with an average weight of 9½lbs (4.31 kg.). Rue observed that the largest fox he had seen was a male which weighed 14 lbs 12 ozs (6.69 kg.), and he also noted a fox from Pennsylvania which weighed just over 16 lbs (7.26 kg.). Similarly Arnold (1956) recorded that the normal weights of foxes (unsexed) from Michigan was from 8 - 12 lbs (3.63 - 5.44 kg.), with an extra large fox weighing up to 15 lbs (6.80 kg.). Rue commented that the weights recorded by Hoffman & Kirkpatrick (1954) were well above the national average.

From the range of weights for European animals, shown in Table 7, it can again be seen that the mean weight of the population does not increase with latitude, contrary to Bergmann's rule, although Haltenorth & Roth (1968) claimed that the weight of the Red fox ranges from 3 - 14 kg. in accordance with Bergmann's rule. However, this upper limit does seem rather high; Fairley (1969) noted a particularly large vixen from Co. Down as weighing 11.6 kg. (25.5 lbs), and this animal was considerably larger than most foxes encountered. As is also apparent from Tables 4 and 7, the longest foxes are not the heaviest.

3.5 SEXUAL DIMORPHISM IN THE WIDTH OF THE HEAD

It is frequently asserted that there is a sexual dimorphism in the width of the head e.g. Talbot (1906), Burrows (1968). Dog foxes are said to have a head that is broader between the ears, and also to have a more domed forehead. Talbot described this as the ears and snout forming a V shape in the vixen and a W shape in the dog when viewed head-on.

In an analysis of the head measurements for 52 dog foxes and 46 vixens killed in London there was no statistically significant difference in the width of the head when expressed as a percentage of the length of the head. This percentage ranges from 38 - 62 in vixens and 33 - 63 in dogs, with a complete overlap in distributions (Figure 3).

TABLE 7

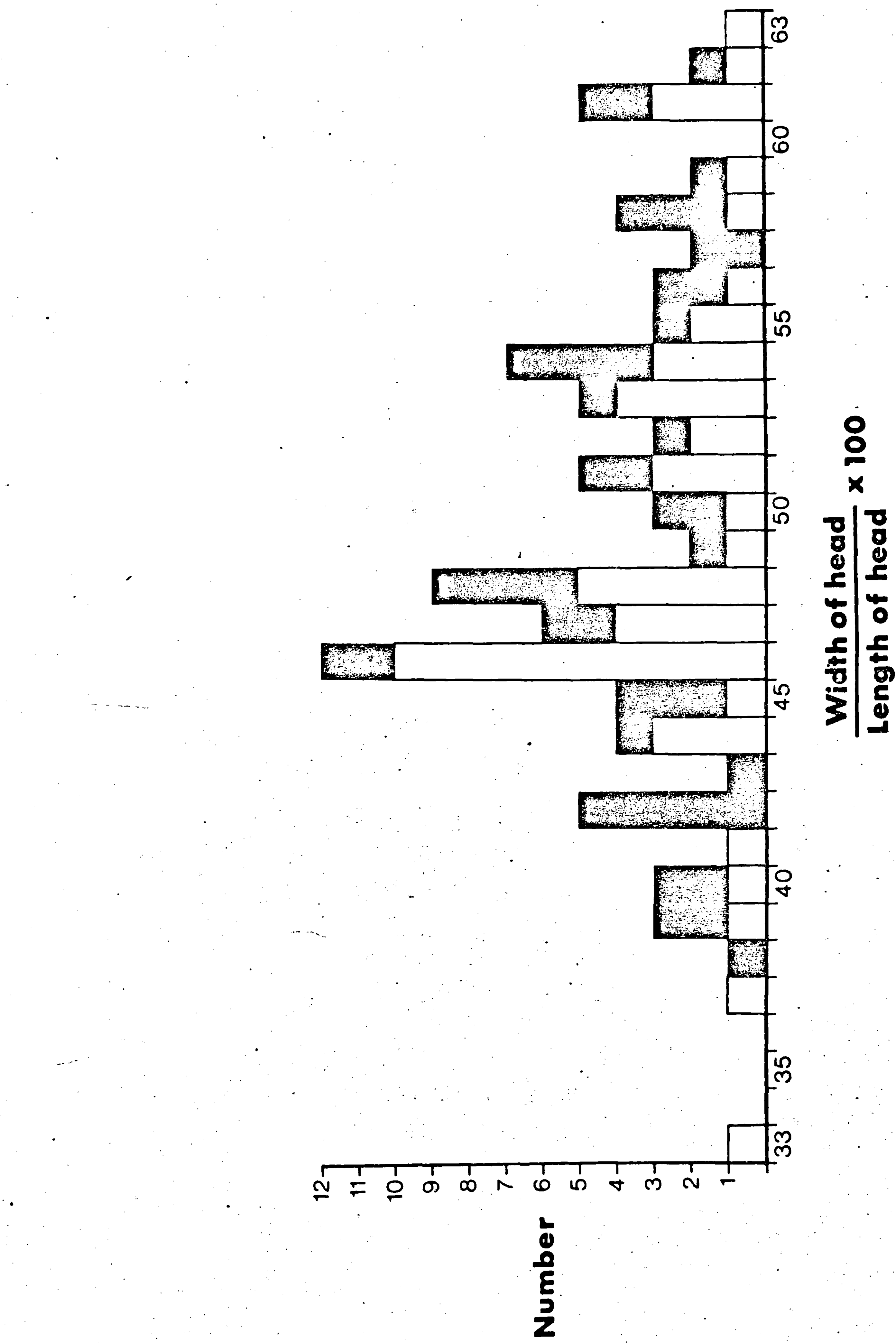
COMPARISON OF BODY WEIGHTS FROM DIFFERENT FOX POPULATIONS. ALL FIGURES ARE WEIGHTS IN KILOGRAMMES.

Source of Material	Dogs		Vixens		Author
	Range	Av	Range	Av	
Kansas	4.08 - 5.67	4.61	2.72 - 4.14	3.99	Stanley 1963 (lbs converted to kilos).
Indiana	3.81 - 6.08	5.25	3.36 - 5.67	4.21	Hoffman & Kirkpatrick 1954 (lbs converted to kilos).
Norway	3.75 - 8.45	5.90	2.12 - 7.80	5.19	Lund 1959.
Netherlands	4.28 - 8.19	5.97	4.00 - 6.80	5.10	Haaften 1970.
London	5.16 - 8.20	6.43	4.00 - 6.77	5.45	Present study.
England	5.5 - 8.2	6.7	3.5 - 6.7	5.4	Hattingh 1956 (reanalysed by Kolb & Hewson 1974).
Northern Ireland	4.0 - 9.2	6.9	4.0 - 6.9	5.8	Fairley 1970.
Scotland	5.7 - 9.3	7.3	4.2 - 7.8	6.2	Kolb & Hewson 1974.
South-west Germany	-	7.0	-	5.5	Haltenorth & Roth 1968.
North-east Germany	-	8.5	-	7.5	

FIGURE 3 SEXUAL DIMORPHISM IN THE WIDTH OF THE HEAD

☐ DOGS

▨ VIXENS


Number
12
11
10
9
8
7
6
5
4
3
2
1
33
35
40
45
50
55
60
63
Width of head / Length of head x 100

Hurrell (1962) and Fairley (1970) both claim that dog foxes have wider snouts than vixens, but taking exact measurements of the width of the snout proved impossible. That dog foxes may have wider snouts is supported by skull measurements. Ognev (1931) noted that skulls from males have a broader rostrum and a broader palate. Churcher (1960) separated Red fox skulls into male and female on indices based on total length, zygomatic width and mastoid width, provided that first and second year animals were considered separately from older specimens. The efficiency of this separation varied between North American populations, and in some populations there was considerable overlap between the sexes.

3.6 SUMMARY

Each fox population exhibited different size characters, evolved to meet its own ecological requirements. The factors that govern body size are complex and simple explanations such as Bergmann's rule do not apply. Suburban foxes are longer in body length and shorter in tail length than most populations with the exception of that from Northern Ireland. There is no corollary between body length, pinna length and hind foot length. However, for their size, suburban foxes are comparatively light, being the same weight (but longer) than English rural foxes, lighter than Scottish and Northern Ireland foxes, and heavier than those from Norway and the Netherlands.

SECTION 4

COMPARISON OF THE TECHNIQUES FOR AGE DETERMINATION, AS APPLIED TO SUBURBAN FOXES

4.1 INTRODUCTION

The ability to determine the absolute age of an animal is one of the most useful techniques available to any wildlife biologist. Alexander (1958) discussed the value of age determination in wildlife management, particularly in relation to interpreting population changes, and he showed that such data are invaluable, particularly in the management of game species. Morris (1972) reviewed some of the recent literature on age determination techniques, and he noted that "without data on an animal's age we cannot establish its rate of growth, the age of reaching maturity, life span and a whole range of factors of vital interest to the wildlife biologist".

Spinage (1973) reviewed the literature on the use of teeth in the determination of an animal's age, placing particular emphasis on African mammals. He also recorded that "knowledge of the ages of individuals is essential to understanding the rates of growth, onset of sexual maturity, fertility peak, senescent decline and life span, as well as social behaviours". Spinage also noted that extreme precision in age determination is often of more academic than practical interest, and that empirically crude methods often suffice.

This last point made by Spinage is only true in certain instances; for studies of productivity, social behaviour, etc. broad age groupings often do suffice, but for studies on population dynamics different generations need to be recognisable. Shilyaeva (1971), for example, studied the structure of Russian Arctic fox (Alopex lagopus) populations, in which he examined the role of different generations in the dynamics of the population. He showed that there were basically three types of generation, corresponding to the three periods of one cycle of arctic fox numbers. Shilyaeva found that generations born in different years, in different living conditions, differed in the rate of multiplication, numbers, structure and life span, the numerically larger generations living less long, but multiplying more briskly, and the numerically small generations having raised indices of life span, fertility, etc.

To be able to recognise separate year classes (= generations in the fox) is also advantageous in the study of disease in a population, and one of the first applications of this technique to the study of the time of appearance and rates of development of a pathological condition in a population is presented in section six of this thesis.

It is not always possible to determine exactly the age of a mammal. Thus Taber (1971), in his review of the criteria of sex and age, noted that in mammals the criteria of age are based on physical maturation, and that there appears to be more variation in this respect between individual mammals than between individual birds. This means that criteria of age are generally somewhat less precise for mammals than they are for birds. Taber also stated that these processes of growth are to some extent controlled by health and nutrition, so that they may be slower in one individual and more rapid in another.

There are several possible methods for the determination of age in the Red fox. Some of these have already been examined briefly, but so far no attempt has been made to correlate the results obtained from these different methods when applied to the same individuals, and to compare the relative effectiveness of these different techniques. Since there is often considerable individual variation in rates of growth and development, absolute reliance on one technique should be avoided if possible - Dolgov & Rossolimo (1966) noted that in determining the ages of animals it is better to use a complex of features.

4.2 INCREMENTAL LINES OF THE DENTINE, CEMENT AND PERIOSTEAL BONE OF THE LOWER JAW

4.2.1 Introduction

The use of this technique has been reviewed in detail by Klevezal' & Kleinenberg (1969), who noted that "this method enables us to determine the age, in years, of every animal and is practically the only method permitting determination of the age of young or old animals of either sex with an error of only up to one year". While this statement is somewhat sweeping, the technique is a very useful one, and it allows the exact determination of an animals age with a high degree of accuracy.

Klevezal' & Kleinenberg noted that since the 1850s the literature has contained data on the presence of layers in the dentine and the presence of ridges on the roots of the teeth of marine mammals. The technique, however, was not utilised for age determination until Scheffer (1950) and Laws (1952) re-examined the technique in Pinnipedia. Scheffer examined the canines of the Fur seal (Callorhinus ursinus), and found that an annual ridge was laid down in the tooth cementum. Laws demonstrated the formation of an annual layer in the dentine of the canines of the Elephant seal (Mirounga leonina).

Since these workers, the technique has been applied to a wide range of terrestrial and aquatic mammals, which includes species from the following orders: Sirenia, Pinnipedia, Insectivora, Chiroptera, Primates, Cetacea, Fissipedia, Perissodactyla, Artiodactyla and Rodentia. A list of references to this work is presented by Madsen (1967), and reviews of the literature are presented by Taber (1963, revised 1971), Klevezal' & Kleinenberg (1969), Morris (1972) and Spinage (1973), and so no similar review will be included here.

Both cement and dentine are laid down oppositionally, dentine on the internal surfaces of the tooth, and cement externally around the root. This means that cement can be deposited without being limited by a lack of space, whereas growth of the dentine in most mammals is a relatively transient process, often ceasing soon after maturity is attained. The exceptions to this are the conical teeth of odontocete whales and the canines of seals, where growth of the dentine is prolonged throughout life (Morris 1972). Most workers have agreed that the use of tooth cementum is a more valuable technique than studying sections of the dentine e.g. Hewer (1964), who studied the Grey seal (Halichoerus grypus), and Gilbert (1966), who studied White-tailed deer (Odocoileus virginianus).

The width of the cement varies from one species of mammal to another. Morris (1972) noted that it was virtually non-existent on the teeth of the hedgehog, (Erinaceus europaeus). In herbivores the cement forms a thick layer, whereas in carnivores this layer is much thinner, but it is still deposited in recognisable annual layers, even the last formed layers of old animals being distinct.

The use of periosteal layers in the bone for age determination is a more recent technique, for which the early literature was reviewed by Klevezal' & Kleinenberg (1969). These authors listed annual layers as occurring in the periosteal bone of the mandible in the following orders of mammals: Insectivora, Lagomorpha, Rodentia, Cetacea, Fissipedia and Pinnipedia. However the technique is of more limited application than growth lines in the teeth, and within one mammalian order the annual lines can be readily demonstrated in one species and not in another. In recent years the technique has been applied with some success to hedgehogs (Erinaceus europaeus) by Morris (1970), and this technique was then applied by Kristoffersson (1971) to hedgehogs in Finland, for which he determined the age distribution of the population. Millar & Zwickel (1972) also used this technique in their study on the age structure and mortality of the pika (Ochotona princeps) in Alberta and Colorado.

Although a large volume of literature now exists demonstrating the presence of growth lines in hard tissues, very little effort has been made to explain the occurrence of these lines. Klevezal' & Kleinenberg (1969) examined the effect of winter on the growth rates of a variety of mammals, and they showed that in most mammals there was a cessation of growth, and sometimes also a loss of body weight (although the Red fox shows an increase in weight in the winter and a loss of weight in the summer (Hattingh 1956, Lund 1959, present study)). Klevezal' & Kleinenberg concluded that all mammals are subject to an annual decrease in the growth rate of the tissues of the teeth and bone, resulting in the formation of annual layers in these tissues. They thought that dark winter lines were formed by a reduction in the rate of growth of the organic stroma of the tissue with no change in the rate of calcification, resulting in narrow winter lines with a high calcium content.

Morris (1970) said that they were "caused by seasonal fluctuations in growth rate", although he did not explain the nature of these seasonal fluctuations. Morris did note that one hedgehog which had not been allowed to hibernate showed no growth lines in the periosteum, and he commented that "dark bands in the periosteal zone, each one corresponding to a period of arrested growth, [are] usually caused by hibernation". While hibernating mammals, such as the hedgehog, showed marked growth lines developed during hibernation, many animals that do not hibernate also show well-developed annuli, although Klevezal' & Kleinenberg (1969) noted that especially distinct annual layers are observed in hibernating mammals.

Sergeant (1967) said "the type of cemental growth is dependent upon nutritional state. Since body growth of captive Cervidae fed a high ration declines at the rutting season, sex hormones reduce food intake and presumably cemental growth also". Mitchell (1967) discussed the growth lines in the cement of red deer (*Cervus elaphus*) from Scotland. He found that the cement pad of the first lower molar consisted of broad layers rich in cementocytes, associated with the summer/autumn period of growth, separated by narrower layers deficient in cementocytes, corresponding with the period of winter/early spring food restriction. Like Sergeant (1967), Mitchell found a correlation between sex hormones and growth lines, and demonstrated the presence of "rutting layers" in some, but not all, stags. Mitchell also pressed the idea that growth lines are not entirely dependent on winter conditions, and noted a lack of an obvious relation between the thickness of the winter layers and the winter conditions. He suggested that his results indicated that the technique may be less effective with animals showing irregular or less seasonal variations in growth.

That physiological state may, on occasions, be important in the development of growth lines was suggested by the rutting lines of some cervids (e.g. Mitchell 1967), but Spinage (1973) noted that despite the fact that oestrogens play a role in calcium-phosphate retention there was little evidence that cementum lines were related to parturition, lactation or sexual activity. The rutting lines of Mitchell could equally well be attributed to nutritional deprivation during the rut. Similarly, the narrow line associated with the moult "haul-out" of Grey seals (Hewer 1964) could equally well be attributed to lack of food rather than change in physiological condition. However Craighead, Craighead & McCutchen (1970) showed that in the fourth premolar of grizzly bears (<u>Ursus arctos</u>) the dark layer was formed from early autumn to May, when the animals are in hibernation, and that there appeared to be no relationship between deposition of the dark cementum layer and low nutrition because bears remained in good physical condition throughout fall and winter. They suggested that an intrinsic mechanism, possibly endocrine, produced physiological changes that caused the formation of the layers - important endocrine changes occur in the grizzly during and immediately following hibernation when the dark layer is deposited. Miles (1961) demonstrated irregular layers in the cementum of human teeth which may have been caused by changes of health (and thereby physiological state), and ill-health (physiological imbalance) causes layering in many human bones.

Klevezal' (1973) compared the patterns of the annual layers in the cement of the beaver (Castor fiber) and the elk (Alces alces), and in the bone and the cement of the mice Apodemus agrarius and A. flavicollis. For each species he compared populations from regions with a marked continental climate with populations from regions with a weak continental climate. He showed that animals from an area with a weak continental climate have poorly developed annual layers, and that counting these layers is more complicated and the data so obtained less reliable.

Klevezal' & Mina (1973) examined the factors that determine the annual layers of teeth and bones, using material from ungulates, carnivores, rodents and cetaceans. They concluded that in mammals which do not hibernate the pattern of annual layers is largely determined genetically and that "the degree of variability of the annual layer pattern in various populations appears to be determined by the value of stabilizing selection pressure, being inversely dependent on it". In most of the cases examined they concluded that the selection factors were seasonal changes of climatic characteristics. Klevezal' & Mina further concluded that the annual layer of adult mammals was not affected by sex or a change of physiological state associated with sex (rut, pregnancy), and neither was the pattern of a given layer peculiar to the specific conditions of the year when that layer was formed.

These views are, however, at variance with those of Robinette & Archer (1971), who examined the cementum pad of the first molar of Thompson's gazelle (Gazella thomsonii) from the equatorial region of Tanzania. They considered that two lines were formed each year, and that one particularly bad drought year produced a recognisable distinct line. Craighead, Craighead & McCutchen (1970) showed that the first five annuli are wider than subsequent annuli in the fourth premolar of grizzly bears, and this phenomen was correlated with physical maturation and the cessation of rapid growth.

The formation of two lines each year seems to be a common phenomenon in African mammals, and this was discussed by Spinage (1973) in his review of the formation of annual layers in African species. In his work on the Ugandan waterbuck (*Kobus defassa ugandae*), Spinage (1967) correlated the formation of two annual layers with the two wet and dry seasons. However, Simpson & Elder (1969) also found two annual lines in the greater kudu (*Tragelaphus strepsiceros*) in southwest Rhodesia, where there is only one dry season each year, and they attributed the two lines to hormonal balance on one hand and nutritional stress on the other.

It is obvious that no satisfactory explanation has been proferred to account for the formation of annual layers, and workers from different climatic areas attribute the formation of annual lines to different causes. The formation of annual lines is, however, a well-documented phenomenon, but with lack of definite information about the underlying causes for their formation some caution must be placed on the interpretation of growth lines.

Although annual incremental lines have been demonstrated in a variety of animals, the technique has been applied to relatively few wild canids. Smirnov (1960), in Klevezal' & Kleinenberg (1969), noted the presence of layering in the cement of the Red fox, Artic fox and wolf, but commented that it did not occur in all specimens.

Dolgov & Rossolimo (1966) described the closure of the pulp cavity of the upper canine of the Artic fox (*Alopex lagopus*) due to deposition of dentine. By this technique they could distinguish between young and old animals, but no exact age was ascribed to the occulsion of the dental cavity. From their data, it seems that the dental cavity was markedly reduced in size in animals entering their second winter, and in animals over two years old it is reduced to a small fine canal. In their winter sample, using this character alone, the population could be divided with a high degree of accuracy into juveniles, animals 1 - 2 years old and older animals.

Klevezal' & Kleinenberg (1969) described their work on the Arctic fox, in which they demonstrated annual layers in the dentine, cement and periosteum of the mandible, and using ranch animals of known age they showed that these layers corresponded to the age of the animal.

In the dentine many accessory bands of various degrees of clarity were found, and these made it difficult to determine the boundary of the annual layer. The tooth cement lines were more distinct, although the first annual layer was considerably less distinct than the succeeding ones. They also found that the number and clarity of the layers in different teeth of the same animal were the same, and that in the canine the cement was considerably thicker in the lower part of the canine but that deposition of cement occurred all over the root and so layers could be counted by cross sections taken from the middle of the root. The periosteal layers of the mandible were best developed in the region of the last premolar or first molar, with the lingual wall sometimes slightly wider. The oldest fox examined was six years of age, and the first layer of the periosteal zone was still not resorbed. To date, this is still the only wild canid in which annual growth lines have been demonstrated in the periosteum and the dentine.

Linhart & Knowlton (1967) studied the coyote (Canis latrans) using 30 known age skulls and the teeth from 156 animals of unknown age. They showed that the permanent canines erupt at 4 to 5 months, and that the root canal closed between the 8th and 9th month. The first opaque layer was formed at 20 - 23 months, and accurate counts were obtained in animals up to 21 years of age. They showed that longitudinal sections were more easily interpreted.

Lombaard (1971) studied the Black-backed jackal (Canis mesomelas) in the Transvaal, and examined both longitudinal and transverse sections of the upper canine, first incisor and first molar. He found that longitudinal sections were more easily interpreted, and that the lines were best developed on the canine teeth. The canine erupted at 21½ weeks of age and the first opaque band began forming at about ten months. The age of an animal was determined by counting the dark layers and adding one year for the first year of life when no dark layer was deposited. After determining the age of his material from these growth lines, Lombaard then compared the results obtained by other techniques.

Jensen & Nielsen (1968) demonstrated the use of cementum lines of the lower canines to determine the age of Red foxes in Denmark. They managed to age 518 out of 522 foxes killed during the winter months. Five wild known-age foxes were used in the study, and from these it was shown that the first dense cementum layer was laid down between the first and second autumn of the life of the animal. They noted that the first layers often consisted of many faint layers, these seeming to become packed together as the animal grew older.

Grue & Jensen (1973) supplied further details on the formation of the lines, using 135 known-age wild foxes, with an age range of 5 months to 4 years. They found a complete correspondence between the number of annuli and the known age in foxes less than one year old and more than three years old. For foxes in their second and third year the technique seemed to be less reliable, showing less distinct dark lines which caused a tendency to underestimate the age. They also showed that from the age of one year, annuli are formed every twelve months in canine tooth cementum, the dense dark line being formed from March to autumn. However this last statement is unlikely to be true, the dark line being formed in the winter but only becoming visible during the summer when less dense cement is laid down outside the dark layer.

Johnston & Beauregard (1969) utilised the technique in a study of rabies epidemiology in Ontario. They ground thin sections of non-decalcified upper left canine teeth, and found that the outer clear band (the dense dark line in decalcified sections) was not well defined until June, when the new cementum had been laid down.

Monson, Stone & Parks (1973) also investigated the use of annual growth lines in the determination of the age of 50 captive and 15 wild

Red foxes in New York State. The known-age animals ranged from 6 months to 3½ years of age. Sagittal sections of premolars and molars were examined, and both sagittal and transverse sections of the canines. They found that premolars were easier to interpret than canines. Based on the canines, accuracy of age determination was 45.7%, whereas using the premolars an accuracy of 90% was obtained when combining the estimates of three observers. No sex difference was noted, but there was a possible increased clarity of layering in wild Red foxes. They concluded that sections of premolars were the most useful, and that a concensus of readings should be taken as the actual age.

Allen (1974) examined the upper canines of 95 known-age wild Red foxes from North Dakota, the age range of the specimens being 0.5 to 3.5 years. He found 100% agreement between the known-ages and the ages assigned by cementum annuli; it was necessary to add 0.5 years to the count of the cementum annuli to obtain the true age of animals collected in the autumn and 1.0 years to an individual collected in late winter. Allen also described a modified technique that reduced the time needed in the preparation of the sections.

The use of incremental lines of dentine, cement and periosteal bone was investigated in the determination of age in suburban foxes, and the ages so obtained were then used as a base-line to compare the usefulness of other age determination techniques.

4.2.2 Preparation of Tooth and Jaw Sections

Whenever possible, the left lower jaw was used. This was cut manually (with a hack-saw) into short sections, each section holding one tooth. In the first specimens the complete jaw length was used, but handling and interpreting of molar sections and periosteal bone from the rear of the jaw proved difficult, and in later specimens only the canine and premolar sections of the jaw were utilised. These sections were then decalcified in a 3% solution of nitric acid in 10% formaldehyde, in open vessels, the decalcifying fluid being changed twice a day. The volume of the decalcifying solution was always at least 50 times the volume of the tissue (Drury & Wallington 1967).

Once the external layers of the bone began to feel soft and spongy, complete decalcification was checked using the technique recommended by Mahoney (1966). When all the calcium salts had been removed, the tissue was neutralised in a 5% sodium sulphate solution for twelve hours, and prior to sectioning the tissue was stored in 70% alcohol.

Sections were cut on a freezing microtome, and varied in thickness from 10 - 30 microns; these sections were cut vertically through the teeth at right angles to the long axis of the jaw. Since the tooth was left in its socket this also gave a transverse section of the jaw. For the canine a transverse section of the root was obtained where it lay beneath the first premolar. In some cases longitudinal sections of the canine root were also cut if interpretation of the transverse section proved difficult.

The sections were held between two microscope slides and stained in Delafields Haematoxylin. They were then mounted in Glycerine Jelly and sealed with Gold Size.

4.2.3 Results

The sections were examined for incremental lines in the periosteum of the lower jaw, in the secondary dentine, and in the cementum of the tooth roots.

In the periosteum many lines were visible, their number increasing in sections taken further back along the lower jaw. The number of these lines showed no correlation with age; sections taken from the same region of the lower jaw in animals of very different ages showed the same number of lines. As a result the technique was abandoned.

Growth lines in the secondary dentine were most easily interpreted in transverse sections (Figure 4d) of the teeth, although they could also be counted in longitudinal sections.

The pulp cavity is closed progressively during the second year of life, when the first dentine line is deposited, and by the end of the second year is reduced to a narrow canal. Thereafter deposition of the secondary dentine is progressively reduced each year, with the result that the annual growth lines become less distinct, and counting such lines is difficult in older animals. This technique was found to be unreliable for animals of four years of age or older, but was invaluable for separating animals in their second summer and autumn from older animals, since the marked difference in the size of the pulp cavity could be determined simply by cutting the canine teeth in half transversely with a hack-saw. In only one older animal (nearly three years of age) was the pulp cavity still pronounced, and this was a pathological condition in which the animal seemed to be suffering from a calcium deficiency (the teeth were hollow shells with poorly defined growth lines).

Only sections of the tooth cementum gave growth lines which could be demonstrated consistently, (Figures 4 to 6), and which could be matched reliably with the age of the animal as roughly estimated by other techniques. For the molar and incisor teeth the growth lines were difficult to demonstrate and usually so closely spaced that accurate counting was difficult. Longitudinal sections of the canine were difficult to interpret near the root, where the lines were more often split and distorted (Figure 4b), although along the length of the canine an accurate count could often be obtained despite the close spacing of the lines. These lines were counted more easily on transverse sections of the canine root (Figure 4d), the growth lines extending along the root to the gum line (although they become progressively crowded as they reach the gum line).

The most useful tooth sections were vertical sections of the premolar teeth, so long as care was taken to ensure that (a) the section was vertical

FIGURE 4 TOOTH SECTIONS

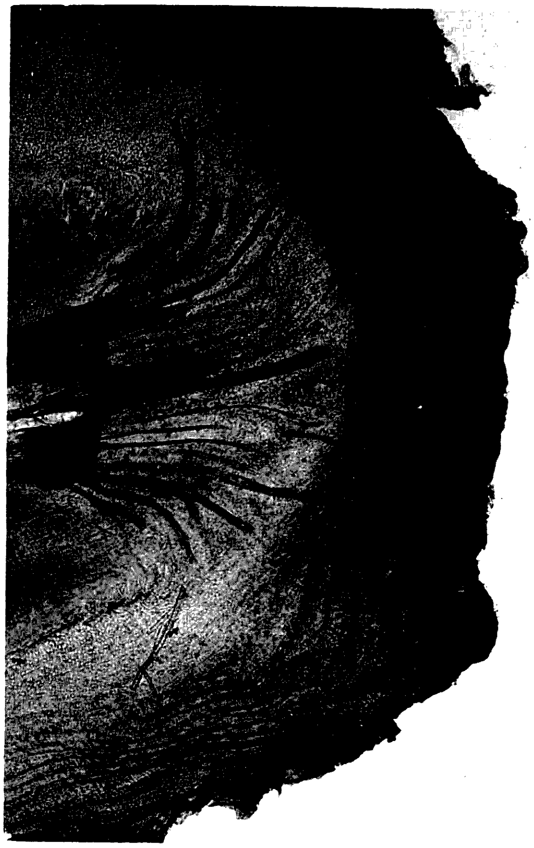
a. SAGITTAL SECTION P2 OF NO. 1002 - ANIMAL KILLED 24-10-1971. FIVE EVENLY SPACED GROWTH LINES ARE SEEN, THE SIXTH ANNULUS ONLY JUST BECOMING DISTINCT.

b. LONGITUDINAL SECTION OF THE CANINE OF THE SAME ANIMAL, SHOWING THE DIFFICULTY IN INTERPRETATION OF SUCH SECTIONS IN OLD ANIMALS.

c. LONGITUDINAL SECTION OF THE CANINE OF No. 1358 - ANIMAL KILLED 4-5-1973. TWO CLEAR ANNULI CAN BE SEEN, THE THIRD IS JUST BEING FORMED.

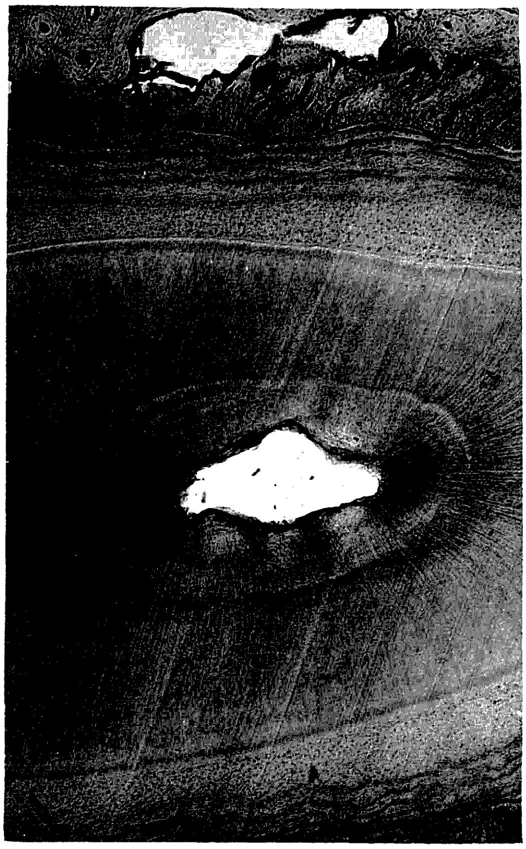
d. TRANSVERSE SECTION OF THE CANINE OF NO. 1271 - ANIMAL KILLED 16-9-1972. FIVE ANNULI ARE SEEN IN THE CEMENTUM; ANNULI IN THE SECONDARY DENTINE ARE MUCH LESS CLEAR.

a.



b.

c.



d.

FIGURE 5 TOOTH SECTIONS

a. SAGITTAL SECTION P3 OF NO. 1099 - ANIMAL KILLED 12-3-1972, AT END OF ITS THIRD WINTER. THIRD GROWTH LINE NOT YET APPARENT.

b. SAGITTAL SECTION P3 of NO. 1188 - ANIMAL KILLED 13-4-1972, ALSO AT THE END OF ITS THIRD WINTER. SECTION IS NOT QUITE VERTICAL AND THE TWO GROWTH LINES ARE MUCH LESS CLEAR THAN IN 5a.

c. SAGITTAL SECTION P3 of NO. 1077 - ANIMAL KILLED 17-2-1972. NO GROWTH LINES CAN BE SEEN AT THE TIP OF THE ROOT, BUT FOUR ANNULI CAN BE SEEN CLEARLY ON THE SIDES OF THE ROOT, WHERE THEY ARE MORE CLOSELY SPACED THAN AT THE TIP OF THE ROOT e.g. 5a.

d. LONGITUDINAL SECTION OF THE CANINE OF THE SAME ANIMAL, ALSO SHOWING FOUR GROWTH LINES, ALTHOUGH THESE ARE SPLIT AND MORE DIFFICULT TO INTERPRET.

a.

b.

c.

d.

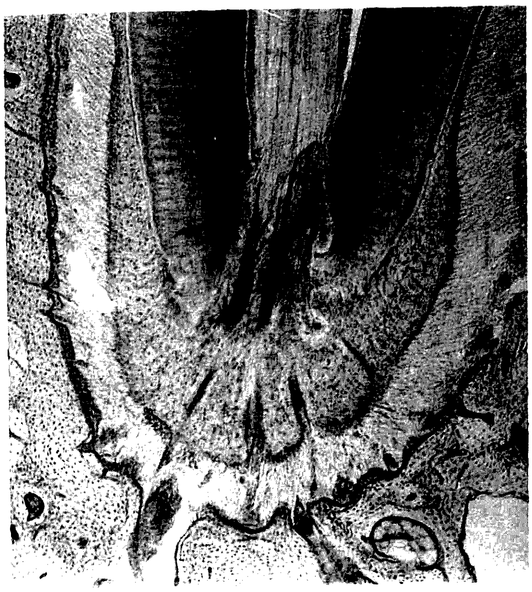
FIGURE 6 DEVELOPMENT OF
AN ANNULUS IN PREMOLAR TEETH

a. SAGITTAL SECTION P3 OF NO. 1050 - ANIMAL KILLED 1-2-1972, AT THE END OF ITS FIRST YEAR OF LIFE. THE FIRST ANNULUS WILL NOT APPEAR UNTIL THE SECOND SUMMER.

b. SATITTAL SECTION P3 OF NO. 1183 - ANIMAL KILLED 30-5-1972. THE FIRST ANNULUS IS JUST BECOMING DISTINCT.

c. SAGITTAL SECTION P3 OF NO. 1317 - ANIMAL KILLED 26-1-1973, WHILE IN ITS SECOND WINTER. ONE GROWTH LINE PRESENT BUT NOT VERY DISTINCT AROUND TIP OF ROOT.

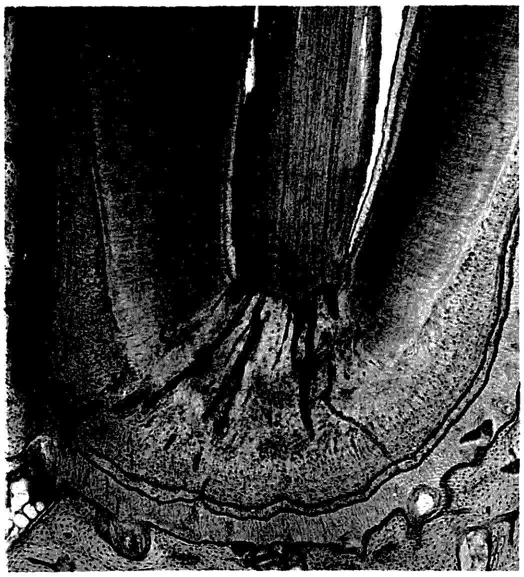
d. SAGITTAL SECTION P2 OF NO. 1082 - ANIMAL KILLED 18-2-1972, WHILE IN ITS SECOND WINTER. ONE VERY CLEAR GROWTH LINE PRESENT - COMPARE WITH 6c.



a.

b.

c.



d.

and (b) that it passed through the root of the tooth (Figures 6a - d). In the premolars the lines are clear, uniformly spaced (even in old animals - Figure 4a), and only very rarely split into the subsiduary lines which make interpretation of the canine sections difficult.

The darkly-staining growth line for the previous winter becomes distinct during the summer, being separated as early as April or as late as August, and so during the summer care must be taken to ensure correct interpretation of the growth lines. The annual line usually appeared first in only one or two teeth, later becoming more distinct in other teeth. Sometimes the line was first detected in the last premolars, at other times in the canine, no set pattern being apparent.

For an accurate assessment of the age of an animal it is imperative to section more than one tooth, since different teeth from the same animal may yield different counts (Table 8), and so the determined age should be based on sections of at least two, and preferably three, teeth.

Subsiduary lines between the annual growth lines make counting and interpretation difficult. To check on the ease and accuracy of interpretation of the sections, a sample of 237 canine and premolar sections from 76 animals were also examined by Dr. G.I. Twigg, who had no previous experience of tooth section interpretation. As shown in Table 9 there was 84% agreement in the interpretation of individual slides, and from Table 10 it can be seen that there was 88.1% agreement in the determination of the age of individual animals, and there was actual disagreement in only 4 (5.3%) of the cases. In these four cases two disagreements were by one year, two by two years. It is likely that after a period of practice by both recorders a greater degree of agreement would be obtained, since the level of disagreement decreased progressively during the trial period. Since this trial sample included mostly summer-killed animals, when interpretation of sections is more difficult, a greater degree of agreement would be expected in a sample of winter-killed animals (which formed the bulk of the material used in this study).

TABLE 8

COMPARISON OF ANNUAL GROWTH LINE COUNTS IN ANIMALS WITH THREE TO FIVE DIFFERENT TEETH (CANINE TO FOURTH PREMOLAR) SECTIONED

	Number of animals	Percent
All sections agree with assessed age	132	82.5
One section disagrees with assessed age	23	14.4
Two sections disagree with assessed age	5	3.1
Total number of animals	160	100.0

TABLE 9

COMPARISON OF SECTION INTERPRETATION BY AN EXPERIENCED AND AN INEXPERIENCED RECORDER

	Number of sections	Percent
Interpretation agreed	199	84.0
One year disagreement	36	15.2
Two years disagreement	1	0.4
Three years disagreement	1	0.4
Total	237	100.0

TABLE 10

COMPARISON OF AGE DETERMINATION BY AN EXPERIENCED AND AN INEXPERIENCED RECORDER

	Number of animals	Percent
Agreement on age determination	67	88.1
Uncertainty on age	5	6.6
Disagreement on age determination	4	5.3
Total	76	100.0

4.2.4 Discussion of Tooth and Jaw Section Data

Despite the absence of annual growth lines in the periosteum of the lower jaw of Vulpes vulpes, Klevezal' & Kleinenberg (1969) have demonstrated these layers in Alopex lagopus (the animals being captive bred). Johnston & Beauregard (1969) also found the mandibular periosteum to be unreliable as an indicator of age in the Red fox, but they did find a more regular deposition of the growth lines in this area i.e. "In areas of the mandible where the periosteal layers were thick, usually two cement lines were observed per year. In areas where the periosteum was thinner, however, usually only one cement line was seen per year. Between these two extremes there were areas where two lines "joined" to become a single line". No such pattern was apparent in the present study.

Dentine layers are rarely used for the determination of age in canids since, as in most carnivores, annuli of the cementum are more distinct. Klevezal' & Kleinenberg (1969) noted that in Arctic foxes there were many accessory bands of various degrees of clarity within the annual layers of the dentine, making it difficult to draw the boundary of the annual layer. In the Red fox Bree, Soest & Stroman (1974) noted that they aged their material by dentine annuli, these being demonstrated by cutting the canine teeth in half, polishing and etching the cut surface and then staining it with toluidin blue. However they did not attempt to show the clarity of these lines, nor the reliability of the technique in age determination. For 176 foxes (79 from the Netherlands and 97 from France) no animal exceeded 50 months of age, despite the occurrence of much older animals in Haaften's (1970) sample of foxes, also from the Netherlands. The present study showed that dentine lines tend to under-estimate the age of older animals, and the observations above suggest that Bree, Soest & Stroman (1974) have also under-estimated the age of their material. Jensen & Nielsen (1968) noted that in their Danish material annuli in the pulp were of irregular occurrence.

In the Red fox the size of the pulp cavity can be used to separate young of the year from older animals, and the value of pulp cavity occlusion for separating animals less than 18 months old from older animals has also been noted in Alopex lagopus by Dolgov & Rossolimo (1966).

Annual incremental lines in the cementum of the canine teeth of the Red fox were first demonstrated by Jensen & Nielsen (1968), and Grue & Jensen (1973) presented further data based on 135 known-age wild foxes. They showed that a single dark line was formed any time from March to the autumn, as in the present study, but they also found that for foxes in their second and third year the technique tended to under-estimate the age of the animals. In the present study by careful reference to the other age data the estimated ages were checked for these age classes, and no tendency to under-estimate age was noted. The results of Grue & Jensen could be attributable to the lower degree of accuracy for canine sections noted in the present study. Grue & Jensen also noted that the accuracy of age determination depends on technically satisfactory sections and on the skill of the observer; the same observations were made in the present study.

Monson, Stone & Parks (1973) in America found that cementum rings in the molars and premolars were more easily and more accurately distinguished and counted than were the rings in the cementum of the canine teeth. This was found to be true of the premolars in the present study, but molars were considered to be unsatisfactory due to the fact that the lines were often closely crowded. Using three observers and known-age material, Monson, Stone & Parks found a 45.7% accuracy in canine tooth interpretation but a 90% accuracy for two out of three observers with the premolar - molar teeth. Most incorrect estimates were only out by a year.

Jensen & Nielsen (1968), Grue & Jensen (1973) and Monson, Stone & Parks (1973) have all demonstrated the accuracy of this technique on known-age material, showing that skill of interpretation is the main source of error. In the present study the reliability of these results has been accepted, and the accuracy of interpretation of the sections checked by a second observer, the results suggesting a maximum of 11.9% of the sample being incorrectly aged, a figure closely parallel to that of Monson, Stone & Parks (1973). Since one observer was relatively inexperienced in interpretation of tooth sections and the most difficult sections were used in the tests this figure is certainly a maximum estimate.

In view of the reliability that can be placed on the age of the animals as determined by tooth cementum layers, this standard was then used to determine the value of other, less time-consuming techniques in the estimation of age in the Red fox.

4.3 USE OF THE BACULUM IN AGE DETERMINATION

4.3.1 Introduction

The baculum is found in male carnivores, pinnipedes, bats, and some rodents and primates (Morris 1972). It can be used as a taxonomic character e.g. Burt (1960), who described the bacula of North American mammals, and it has been used for age determination in some species, notably some pinnipedes (e.g. Hewer 1964), carnivores of the families Ursidae (e.g. Rausch 1961), Mustelidae (e.g. Walton 1968), Canidae (e.g. Lombaard 1971) and Procyonidae (e.g. Sanderson 1961), and in some rodents, such as thebeaver (Castor canadensis michiganensis) (Friley 1949), the Bank vole (Clethrionomys glareolus) (Artimo 1964) and the Musk rat (Ondatra zibethica) (Elder & Shanks 1962).

The early work of Deanesley (1935) on the stoat (Mustela erminea) and of Wright (1947, 1951), on the Long-tailed weasel (Mustela frenata) showed that growth and form of the baculum is related to increased levels of sex hormones, the bone growing throughout puberty so that the mature form of the baculum is attained during the first breeding season. Deanesley also showed that the change in the baculum from immature to mature type occurred over a period of about a month. Sanderson (1961) showed that final maturation of the baculum in the raccoon (Procyon lotor) is dependent on the sex hormones, and that castrated males had a baculum that was juvenile in its character, being much shorter and thinner than one from an intact animal of comparable age. The sex hormones were found to have little or no effect on the raccoon baculum prior to the animals reaching seven months of age. In his study Sanderson demonstrated considerable individual variation in the size and conformation of the baculum, but despite this variation during the hunting season he was able to classify male raccoons into juvenile or adult animals, with only 3 - 6% of the animals being classified as intermediate.

Similarly Walton (1968) could distinguish juvenile from adult polecats (Putorius putorius) during the latter half of the year, but from January onwards the samples were of mixed ages. Walton gave no details on the degree of separation of the autumn sample. Occasionally a greater degree of success is encountered - Friley (1949) classified the bacula of his Michigan beavers into three age classes (yearlings, two- and three-year olds, and four-year olds plus).

Most authors have shown that the general pattern of growth of the baculum is of a rapid growth in length in juvenile animals, the growth in length slowing at the onset of puberty and the bone becoming thicker and heavier under the influence of the sex hormones.

The baculum has been studied in a few wild canids, but with only limited success when applied to age determination. Dolgov & Rossolimo (1966) studied the Arctic fox (Alopex lagopus). They found that there was a great variation in the form and size of the baculum, that of first year animals being particularly distinct. From their data, in which they used a weight to length ratio, it appears that animals up to a year old were distinct from the animals of the previous year, when comparing animals sampled at the same time of the year, but thereafter the samples were mixed.

Lombaard (1971) examined the baculum of the Black-backed jackal (Canis mesomelas). He showed that immature and mature bacula looked alike, and that no change in shape could be observed from the age of two weeks to five years. Monthly samples showed considerable overlap in length and weight measurements. He found that the weight and length of bacula of specimens less than five months old were always lower than for year-old specimens; those of specimens six and more months old were indistinguishable from adult bacula. On this basis Lombaard noted animals younger than five months to be immature, and those older than five months as mature, the maximum weight and length of the baculum being achieved quite rapidly between the fifth and sixth months.

Bree, Chanudet & Saint Girons (1966) studied 126 fox bacula from France, and suggested that foxes whose bacula had reached a length of 50 mm were at the beginning of puberty, and that those in which the weight of the baculum exceeded 0.5 gms must be considered to be sexually mature (age class 9 - 12 months and older). In a correcting note, Bree, Chanudet, Saint Girons & Stroman (1973) used material from the Netherlands. After sectioning the lower left canine to determine the exact age of the animal, they modified their views, reporting that foxes with a baculum longer than 45 mm and heavier than 400 mg. were sexually mature. They also noted that Netherlands foxes are generally a little "sturdier" than French foxes, and so they considered that the lengths and weights given applied to French animals with an even more marked safety margin. They also recorded that foxes become sexually mature during the first winter after birth, and in consequence the limit given applied to animals more than nine months old. However they made no attempt to present data showing the degree of separation of juveniles 6 to 9 months old from adult animals, this being the important age at which the young of the year enter the adult population. They presented a graph showing the growth of the baculum, but no time scale was given to this graph. However, it appeared that there was considerable overlap between the baculum size of juvenile and adult animals.

4.3.2 Preparation of the Bacula

The penis was removed, and the bulk of the flesh was cleaned off using a pair of scissors and a blunt scapel, taking care not to damage the surface of the bone. The bone was then boiled gently in a 10% solution of sodium perborate to remove any remaining meat and to bleach the bone. If any fat was left, this was removed with acetone.

The bacula were measured with a pair of calipers to the nearest 0.1 mm, and weighed to the nearest milligramme. Some bacula exhibited old injuries, possibly as the result of fights, and were discarded.

4.3.3 Results

Description of baculum: The Red fox baculum is similar to the baculum of most other canids. It lies along the length of the penis, as in *Canis mesomelas*(Lombaard 1971) and *Canis familiaris* (Miller 1952). The three regions of the baculum (head or base, body and tail or apex) are slightly more distinct than in *Canis mesomelas*, the bone being similar in general appearance to the baculum of some breeds of dog. The base is smooth in young animals, becoming roughened and more pronounced with age. There is a deep urethral groove along the ventral side of the body, which extends from $^2/_3$ to $^4/_5$ of the length of the bone, which causes this part of the baculum to be V shaped in cross-section. The caudal end of the bone is bent ventrally through an angle of 10° - 30°, and several minor bends may occur along the length of the bone, this usually being a double bend as Dolgov & Rossolimo (1966) described in *Alopex lagopus*. The tail of the bone is flattened or oval in shape, and is often bifurcated at its apex.. In *Alopex* Dolgov & Rossolimo (1966) claimed that the bifurcation deepened with age; in the Red fox the reverse trend was evident but could not be quantified. In young animals a strip of fibro-cartilage a few millimetres in length continues to the end of the glans penis, but this progressively disappears with age. Again this could not be quantified.

The young baculum exhibits the same general shape, but it is made of porous bone and is fenestrated. During growth there is no change in shape, and some of these apertures in the bone may persist in some adult animals.

Use of the baculum for age determination: From Figure 7, it can be seen that the Red fox baculum undergoes a period of rapid growth in length, until a length of 40 millimetres and a weight of 200 milligrams is reached. This size is attained by late September, when the animals are six months old. From that period the growth of the testes accelerates with the approach of the breeding season, and concomittantly the baculum begins to undergo an increase in weight with little increase in length. This growth in weight occurs throughout life, although at a decreasing rate.

For the separation of year classes the weight is obviously the more useful measurement, but as Figure 7 shows any animal with a baculum weight in excess of 275 mgms (and a length in excess of 42.5 mm) may be either a first- or second-year animal, and any animal with a baculum weight in excess of 400 mgms (and a length in excess of 45.0 mm) may belong to any of the eight year classes encountered.

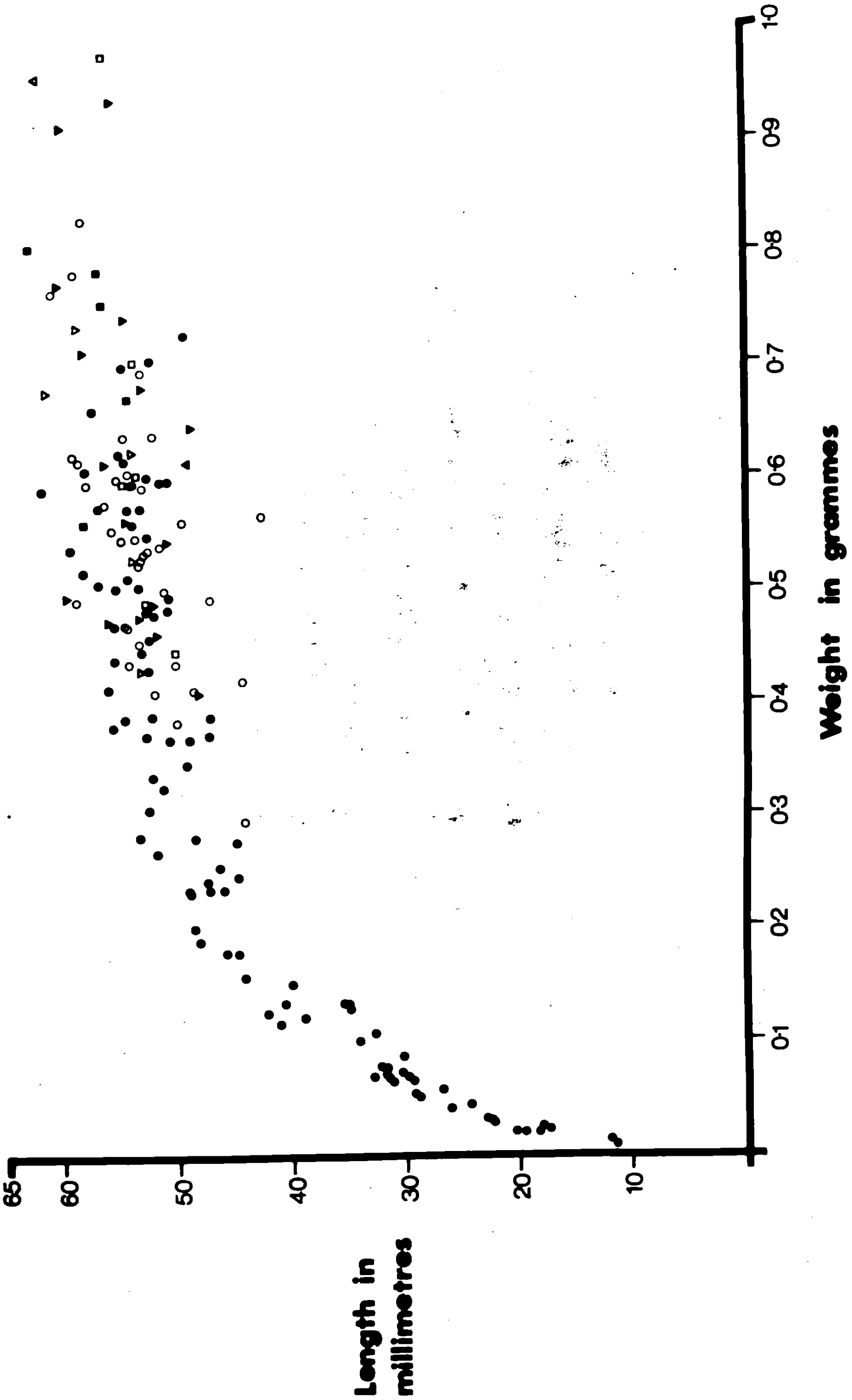
There was a general increase in weight of the baculum with age, but with the sample divided in half-year classes there was a considerable overlap in both the range of weights and also their standard deviations, so that the separation of age classes was not possible.

A variety of baculum indices based on a ratio of the weight and length measurements, as utilised with success by Hewer (1964), Bree, Jensen & Kleijn (1966) and Dolgov & Rossolimo (1966), were tried, but no separation of year classes could be achieved, even when comparing monthly samples.

Comparing the baculum weight of three-monthly samples (Figure 8)

FIGURE 7 GROWTH OF THE BACULUM WITH AGE

● FIRST YEAR CLASS
○ SECOND YEAR CLASS
▼ THIRD YEAR CLASS
▽ FOURTH YEAR CLASS
■ FIFTH YEAR CLASS
□ SIXTH YEAR CLASS
▲ SEVENTH YEAR CLASS
△ EIGHTH YEAR CLASS


Length in millimetres
65
60
50
40
30
20
10
0·1
0·2
0·3
0·4
0·5
0·6
0·7
0·8
0·9
1·0
Weight in grammes

it can be seen that 100% separation of juvenile and adult animals can only be achieved to the end of September, when the young of the year are only six months old. From October to December the sample of bacula (25) weighing less than 600 mgms consisted of 20 (80%) first-year animals, 4 (16%) second-year animals and 1 (4%) third-year and older animals. No first year animal had a baculum weight in excess of 600 mgms. In the January to March sample first-year animals exhibited baculum weights up to 750 mgms, and showed a complete overlap with older animals; of these 57 animals with a baculum weight of less than 750 mgms 31 (54.4%) were first-year animals, 13 (22.8%) were second-year animals, and 13 (22.8%) were third-year plus animals.

Older bacula can be recognised by an increased roughening to the base, but such characters were not quantifiable.

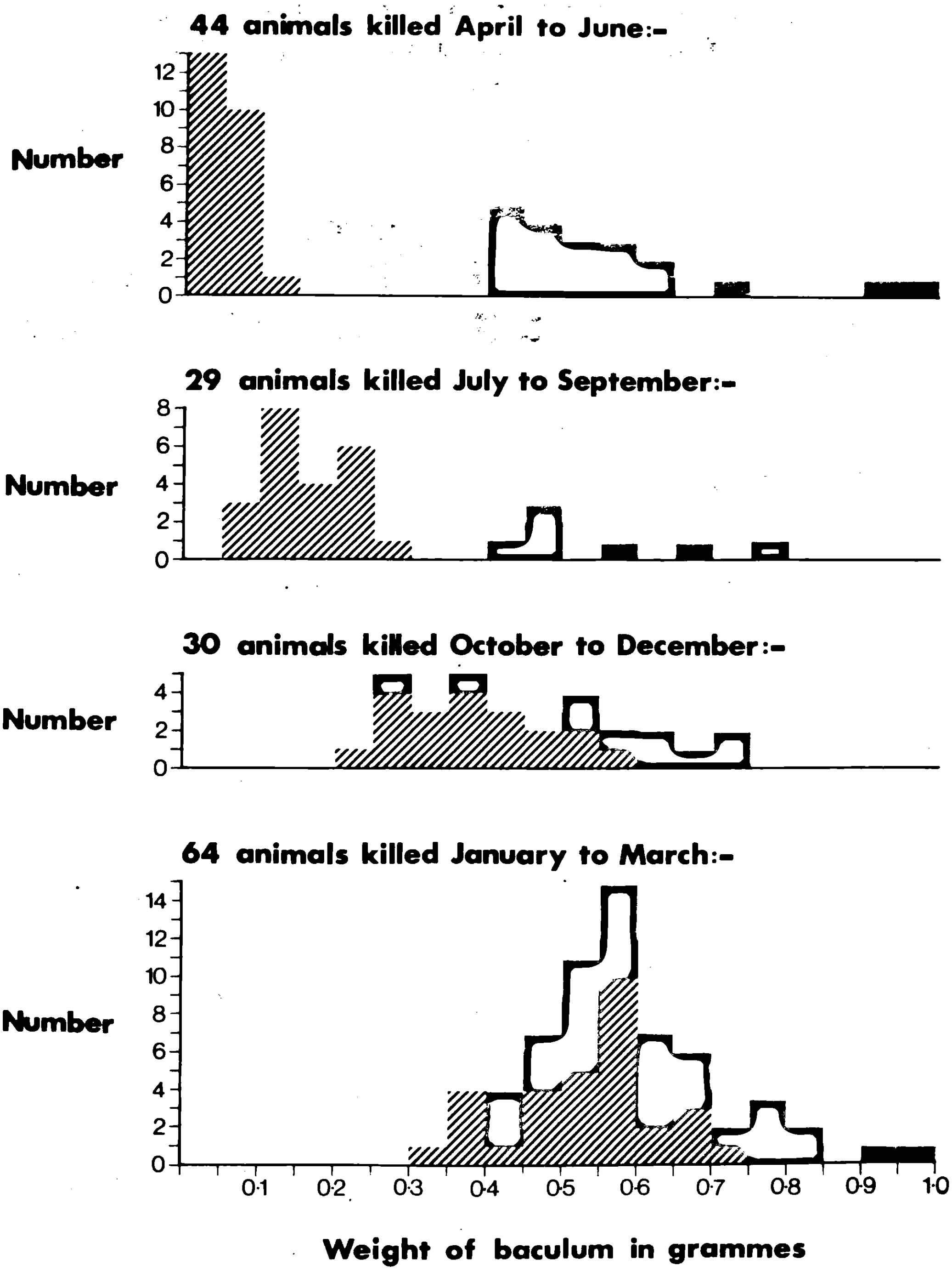
4.3.4 Discussion of Baculum Data

The baculum in canids offers little help in age determination. Lombaard (1971) noted that in Canis mesomelas the baculum could only be utilised to separate animals of five months of age or less from older animals, and a similar result was obtained in the present study, only animals less than six months old being separable on this character. Greater success was achieved by Dolgov & Rossolimo (1966) with the Arctic fox, in which they could separate animals less than twelve months old from older animals.

The data presented by Bree, Chanudet, Saint Girons & Stroman (1973) suggests that for the Red fox the baculum can be used to distinguish animals less than nine months old. However their sample was small (less than 50 known-age animals) and their data do not agree with the results presented here. They noted that animals with a baculum weight in excess of 400 mgms (and a length more than 45 mm) were sexually mature (i.e. over nine months of age). In the present study a random sample of 30 male foxes killed during October to December contained 16

FIGURE 8 BACULUM WEIGHT IN DIFFERENT YEAR CLASSES, COMPARING THREE-MONTHLY SAMPLES

▧ FIRST YEAR CLASS
■ SECOND YEAR CLASS
▒ THIRD YEAR AND OLDER


44 animals killed April to June:-
Number
0
2
4
6
8
10
12
29 animals killed July to September:-
Number
0
2
4
6
8
30 animals killed October to December:-
Number
0
2
4
64 animals killed January to March:-
Number
0
2
4
6
8
10
12
14
0·1
0·2
0·3
0·4
0·5
0·6
0·7
0·8
0·9
1·0
Weight of baculum in grammes

animals with a baculum weight in excess of 400 mgms; of these 8 (50%) were animals only 6 - 9 months old and not sexually mature according to Bree, Chanudet, Saint Girons & Stroman. The slightly larger weight of London foxes over these from the Netherlands (Section 3) does not explain such a discrepancy. In the same sample of London foxes a second-year animal had a baculum weight of less than 300 mgms. Since London dog foxes have an average weight 8% heavier than dog foxes from the Netherlands (Table 7), it is surprising that second-year London foxes can exhibit a baculum so much lighter than that said to typify a sexually mature dog fox from the Netherlands.

Despite the more optimistic views of other authors, the baculum can only be used to separate reliably animals less than six months old from older animals. Since most foxes are sampled in the winter months it is most useful to be able to separate animals 7 - 12 months old (the young of the year) from older animals, and so the technique is of little application in a study of population dynamics.

4.4 USE OF THE EYE LENS WEIGHT IN AGE DETERMINATION

4.4.1 Introduction

Friend (1967) reviewed the literature on research on eye-lens weights as a criterion of age in animals. He described the early work on the human eye lens, describing studies since 1720 and noting that Smith (1883) made the important observation that the growth of the lens does not cease with that of the rest of the body but that its growth is continuous throughout the whole period of life. This pattern of growth is typical of ectodermal structures, but because of its unusual position in the body little if any of this additional lens material is worn away, so resulting in a steady increase in size (Morris 1972). This important concept is the basis on which the eye lens weight is used for age determination. As an example of this process Friend noted the work of

Collins (1905), who recorded an increase in lens weight for humans from birth to eighty years of age.

There were some early studies of the growth of the eye lens in laboratory animals, notably white Norway rats (*Rattus norvegicus*), but the first study of the growth of the eye lens in a wild animal was that of Lord (1959), who found that in the cottontail rabbit (*Sylvilagus floridanus*) the weights of formalin-fixed, oven-dried lenses could be used for age determination. Since then the technique has been applied to a wide variety of mammals and birds (Friend 1967).

This has proved a successful technique for many species, either allowing for a separation of the young-of-the-year from adults, or sometimes even allowing separation of year classes e.g. Longhurst (1964) with Columbian black-tailed deer (*Odocoileus hemionus columbianus*) in which he was able to separate at least the first five year classes.

The eye-lens weight has been utilised as a means of age determination in relatively few species of canids. Lord (1961) examined the eyes of 104 Gray foxes (*Urocyon cinereoargenteus floridanus*) from Florida. He found that there was a 78% agreement between lens weight and tooth wear techniques when both were used to estimate the year of birth of the foxes, and that there was a 90% agreement when the two techniques were simply used to distinguish between juvenile and adult foxes. He made no attempt to determine the usefulness of the technique and the percentage separation between the different age classes.

Lord (1966) also examined the growth of the eye lens in 42 Pampas gray foxes (*Dusicyon gymnocercus antiquus*) and in 175 Patagonian gray foxes (*Dusicyon griseus griseus*). The data obtained were plotted on a frequency distribution histogram and Lord assumed that each peak represented an age class. However he had no reason to make this assumption, and neither did Lord make any attempt to determine the usefulness of the technique in age determination.

Friend & Linhart (1964) examined the technique in the Red fox, using 72 known-age Silver foxes and 458 wild Red foxes collected in New York state. They concluded that juveniles could be separated from adults by this technique with "a high degree of accuracy", but that the separation of age groups among adults appeared remote. However when Johnston & Beauregard (1969) tried to apply this technique to Red foxes in Ontario they found that there were inconsistencies in paired lens weights which far exceeded the expected variation, possibly due to the variation in the initial handling of specimens before fixation in the laboratory; they abandoned this technique. In contrast Haaften (1970), using the dried eye lens weight, was able not only to separate juveniles from adults but was also able to age the adults, and presented convincing data for animals up to eight years of age. The usefulness of the technique for the Red fox is therefore subject to some debate.

Lombaard (1971) examined the eye lenses of 64 known-age Black-backed jackals (Canis mesomelas). He found that 39% of the paired lenses weighed the same or only differed by less than 1% from the mean weight of the two lenses, but that the eye lens weight was only useful for separating those jackals less than 30 weeks of age from those of more than 30 weeks. However Lombaard washed the fixed eye lenses in tap water before weighing and this introduces a variable factor which may reduce the reliability of his results.

4.4.2 Preparation of Eye Lenses

Friend (1968) has summarised the sources of variation inherent in this technique, and Morris (1972) expanded slightly on this, discussing the handling of eye lenses. The following procedures were rigidly adhered to:-

1) The entire eyes were removed within 24 hours of death from unfrozen specimens only, and thereafter the two eyes were handled separately.

2) The eyes were fixed in a 10% neutral solution of formaldehyde, and a ratio of at least 10 : 1 by volume of fixative to tissue was used. A $\frac{1}{2}$" slit was made in the back of the eye-ball to allow easy penetration of fixative.

3) Fixation was carried out for exactly 30 days in a cool room.

4) The eye was then cut open, the lens removed, air-dried, and then dried in an oven at 80°C until a constant dry weight was obtained.

5) Since the lenses are hygroscopic, they were cooled in a desiccator over anhydrous calcium chloride, and only removed briefly for weighing.

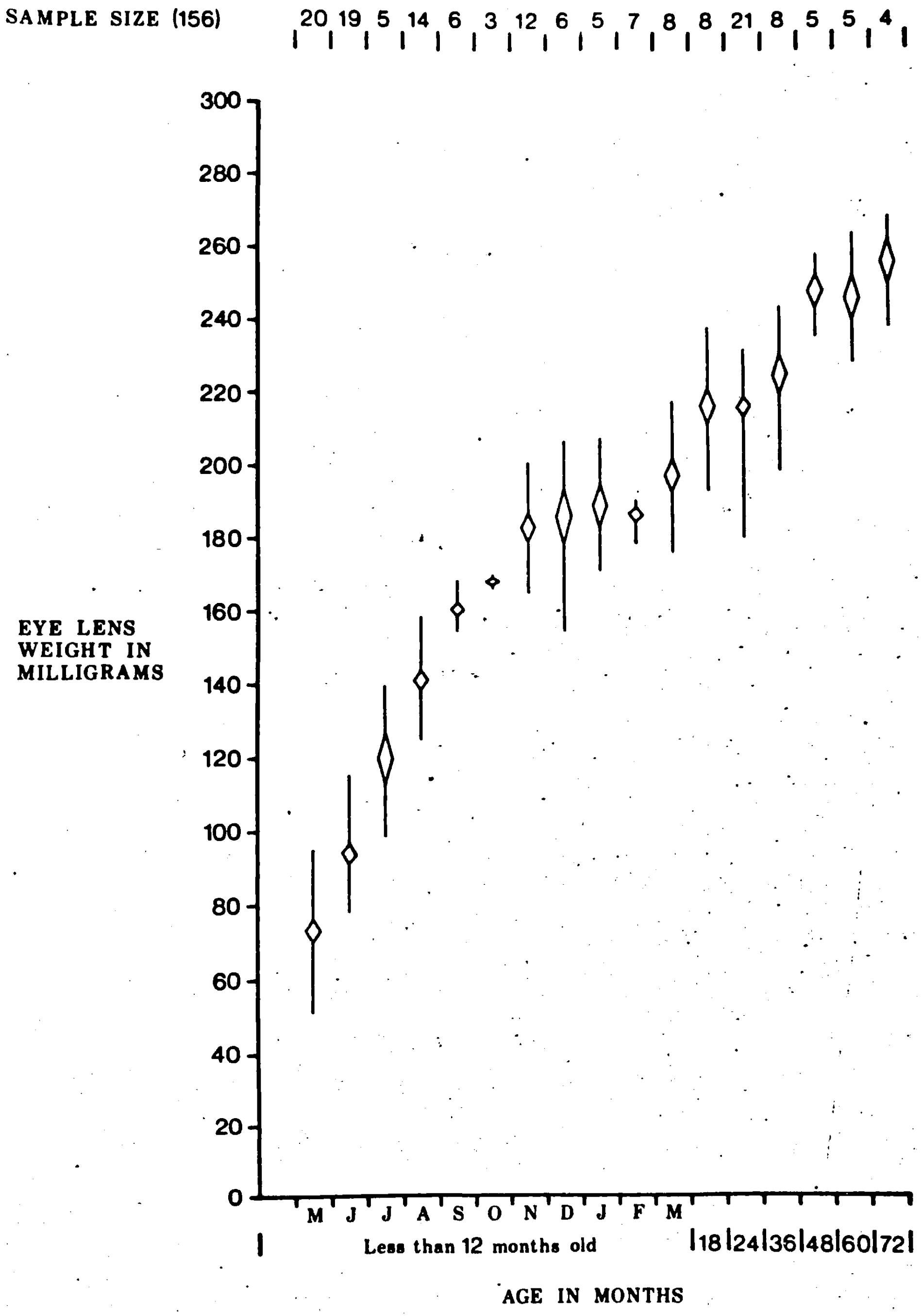
6) For age-determination purposes the recommendations of Morris (1972) were followed, only lenses with no external signs of damage being used, and the two lenses had to differ in weight by only 1% or less (Lord 1959). A large number of animals were shot in the head, so that one of the eyes was damaged. In these cases, the remaining eye lens was used if it showed no external signs of damage, but less reliance was placed on the results so obtained.

4.4.3 Results

In all 144 pairs of lenses differing in weight by 1% or less was prepared. A further 30 single undamaged lenses were also collected. The growth of the eye lens with age is shown in Figure 9. - since no sex difference was found both sexes were grouped together on the diagram.

From Figure 10 it can be seen that there is a complete separation of young of the year from older animals up to the end of September. During the winter months (October to March) only one animal less than a year old had an eye lens weight in excess of 210 mgms (217. 3 mgms), and 210 mgms was taken as the separation point between juveniles and adults. In the three-month sample October - December 21/23 (91%) of

FIGURE 9 GROWTH OF THE EYE LENS WITH AGE, SHOWING THE AVERAGE, STANDARD ERROR (LOZENGE) AND RANGE OF READINGS


SAMPLE SIZE (156)
20 19 5 14 6 3 12 6 5 7 8 8 21 8 5 5 4
EYE LENS WEIGHT IN MILLIGRAMS
300
280
260
240
220
200
180
160
140
120
100
80
60
40
20
0
M J J A S O N D J F M
Less than 12 months old
18 24 36 48 60 72
AGE IN MONTHS

the animals with an eye lens weight of less than 210 mgms were less than a year old, and for the January - March sample 21/25 (84%) were less than a year old. Thereafter there was a complete overlap between age classes.

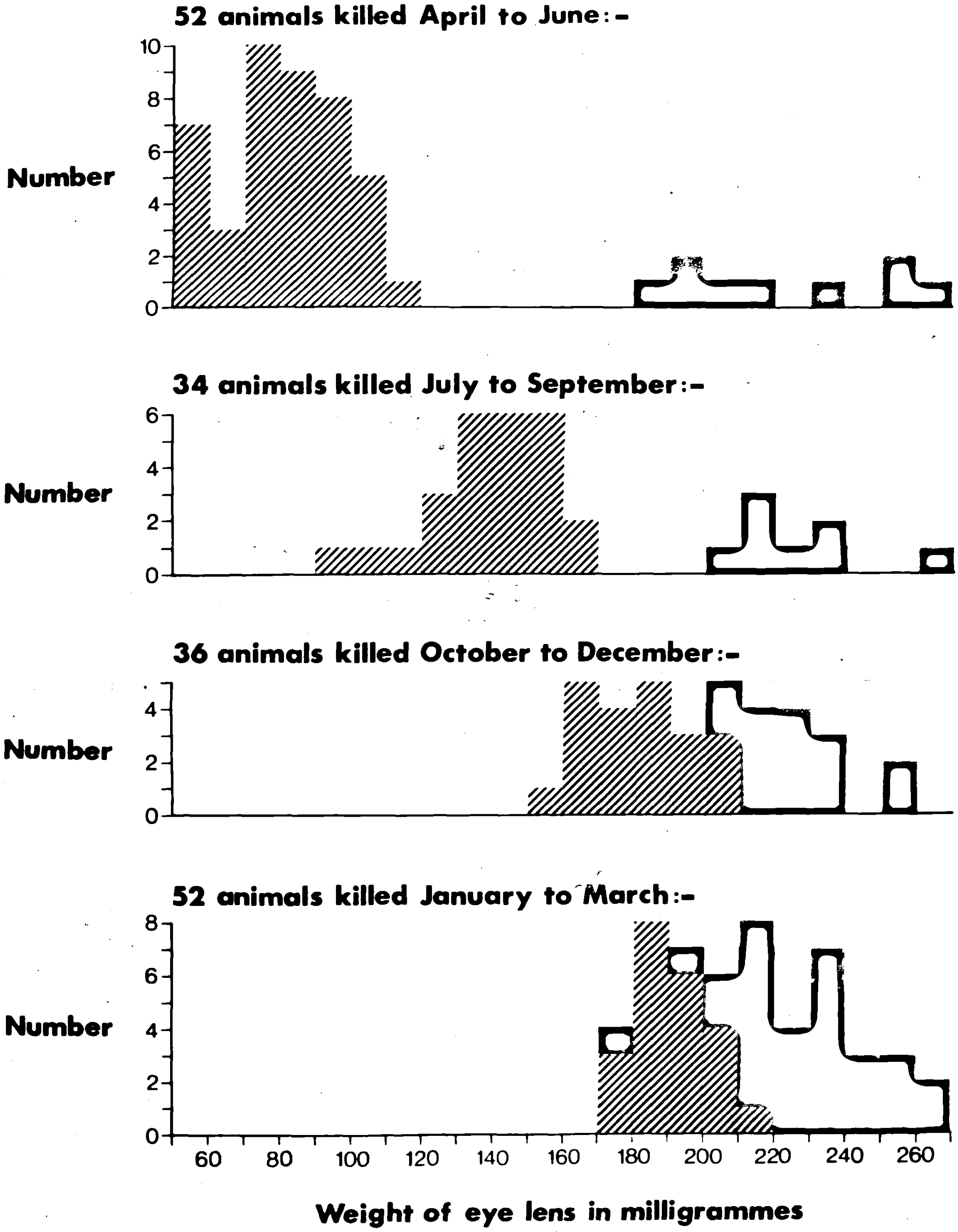
4.4.4 Discussion of Eye Lens Weight Data

Friend & Linhart (1964) also found that the separation of juvenile from adult Red foxes occurred with an eye lens weight of 203 - 213 milligrammes; it is interesting to note the same separation point between London foxes and American foxes when the two samples vary markedly in body size (Section 3). Friend & Linhart also found that for 78 specimens there was complete agreement between eye lens data and degree of ossification of the proximal epiphysis of the humerus. However their sample was collected only in September and October, and the same success in separating juveniles from adults in the late autumn was found in the present study. At that time of the year many techniques are equally applicable and later in the winter, when more animals are sampled, less reliable separation of young of the year from adults was achieved using eye lens weight. Friend & Linhart, with a sample limited to only a few months of the year, over-estimated the value of this technique. The data presented by Haaften (1970) was convincing for his population; why he obtained such good results is difficult to explain but presumably his animals were sampled from very uniform environmental conditions - no details of the sample were given.

The eye lens technique also suffers from the disadvantages of being time-consuming and also being limiting in that only very fresh animals can be aged. In the present study many animals had been shot in the head, thereby rendering one or both eyes unusable, and this also limited the usefulness of the technique.

FIGURE 10 EYE LENS WEIGHT IN DIFFERENT YEAR CLASSES, COMPARING THREE-MONTHLY SAMPLES

▨	FIRST YEAR CLASS
▣	SECOND YEAR CLASS
░	THIRD YEAR AND OLDER


52 animals killed April to June:-
34 animals killed July to September:-
36 animals killed October to December:-
52 animals killed January to March:-
Number
Number
Number
Number
0
2
4
6
8
10
60
80
100
120
140
160
180
200
220
240
260
Weight of eye lens in milligrammes

4.5 USE OF TOOTH WEAR IN AGE DETERMINATION

4.5.1 Introduction

Tooth attrition is one of the oldest techniques for age determination, being particularly applicable to large herbivores. The degree of attrition of the permanent teeth is either determined visually by comparing a series of known-age material, or by measuring tooth height. As Spinage (1973) pointed out, such measurements are only pseudo-objective since although measurements may remove observer bias they do not eliminate variations due to individual rates of wear. Spinage also noted that the pattern of attrition should tend to follow a negative exponential rate of decay, so that a rapid rate of wear in the younger classes makes them look older, whilst flattening of the curve in the older classes makes them difficult to separate from younger ones. Examples of this are seen in Odocoileus virginianus (Ryel, Fay & Etten 1961), and in Odeocoileus hemionus (Erickson, Anderson, Medin & Bowden 1970). Silver (1969) noted that in the horse between five years and seven years the incisors wear at a rate of ¼" per year while later in life the rate is much reduced so that over 20 years of age, the incisors wear at a rate of ¼" per five years.

The use of tooth wear has been used for some time to determine the age structure and productivity of a variety of ungulates e.g. as long ago as 1932 Cahalane described this technique in the White-tailed deer (Odocoileus virginianus). Since the development of the use of incremental lines for age determination, several attempts have been made to determine the validity of these tooth-wear standards in age determination. Boozer (1969) examined Odocoileus virginianus and found a 72% agreement between cementum annuli and tooth-wear techniques, and 88% agreement within plus or minus one year. Keiss (1969) obtained a 50% agreement between the ages determined by tooth wear and cementum lines in American elk (Cervus canadensis), and he also noted that for tooth wear some estimates were as much as seven years out. These and many other authors have expressed doubts as to the validity of the degree of tooth wear as assessed visually. Other authors e.g. Quimby & Gaab (1957), with elk, are of the opinion that visual estimation is a reliable technique, and Novakowski (1965) found incisor wear to be a useful field technique in bison (*Bison bison*).

For a full review of the technique as applied to herbivores see Taber (1971) and Spinage (1973); Spinage also discussed the draw-backs of the technique in some detail.

Few attempts have been made to determine the age of canids using tooth attrition. Gier (1968) aged coyotes (*Canis latrans*) using wear of the upper and lower incisors and canines, and included a diagram showing the degrees of wear of these teeth in animals up to eight years old. However he made no attempt to determine the degree of accuracy of his technique. Silver (1969) noted that in the Domestic dog (*Canis familiaris*) at one year all the incisors are in wear but still have the *fleur-de-lys* shape which is completely lost by two years. Lombaard (1971) used the same technique for determining the age of Black-backed jackals (*Canis mesomelas*) but only used the upper incisors. In describing the wear of these teeth by year classes he noted that in two year old animals the first signs of wear started to appear on I^1 and I^2, and that in animals of seven years of age and over no cusps or fissures remained; furthermore, in some animals the teeth were worn down to the gum line, so that age determination by means of the degree of attrition of the upper incisors could not be used for animals of seven years and over. Lombaard also noted that tooth wear of the upper incisors was influenced by the loss of contiguous teeth, and the loss of upper or lower incisors on the one side of the jaw increased tooth wear markedly on the opposite side of the jaw, and that the more teeth that are lost the greater the wearing stress on the remaining teeth.

Gurskii (1973) described age changes in the skull of the wolf (*Canis lupus*). He noted that the upper incisors and canines were all clean with sharp apices in animals 2 - 4 years old, the first signs of wear appearing in the 4 - 6 year age class. He noted that with abnormal bites the rate of attrition was markedly increased.

In the various foxes examined, Dolgov & Rossolimo (1966) noted that in the Arctic fox (Alopex lagopus) tooth wear proved unreliable as an index of age due to the self-inflicted damage caused by live-trapping.

Markina (1962) described the sequence of wear of the teeth in the Red fox (Vulpes vulpes), although he made no attempt to correlate this with age. He noted that the sequence of wear of the teeth depends on whether the teeth of the upper and lower jaws are in contact, and that teeth that undergo friction and a more constant load are worn down more quickly i. e. incisors, canines and carnassial teeth. He described also how tooth wear depends largely on the changing load on the different teeth in relation to the food of the individual animals, so causing individual variation in the wearing down of the teeth. As a result specimens are found with incisors worn down to the dentine but with the molars not worn down, and vice versa. This must be born in mind when taking account of tooth wear during age determination. Markina found that the incisors showed the first signs of wear, this appearing at about one year of age.

Wood (1958) aged the Gray fox (Urocyon cinereoargenteus) by tooth attrition. He checked the wear on the incisors, canines, carnassials and crushing molars, but found that only the latter teeth showed promise for an age criterion, and the character selected was the degree of wear on the protoconule and metaconule of the first upper molar. He noted five degrees of tooth wear which he thought were correlated with year classes. For 44 known-age readings he found a 93.2% correlation with estimated age.

For the Red fox Stubbe (1965) modified this scheme, recognising four distinct age groups for his material, which was sampled only in the autumn, so facilitating separation of age classes. Bree, Soest & Stroman (1974) examined the techniques of Wood and of Stubbe, using material from the

Netherlands and from France, having first determined the age of their material by means of dentine layers of the canine teeth. They found that only 35% of the Netherlands foxes and 47% of the French foxes were aged in accordance with their objective age, but most errors were not in excess of one year. They concluded that age determination by tooth wear characteristics was considered an unreliable method by which to study the age structure of a carnivore population, and that the great variability in the wearing process is probably due to such factors as the genetic background of the individuals, the size of the litter from which they originated, the structure and the calcium content of the food taken and the inidividual variation in calcium metabolism.

4.5.2 Recording Tooth Attrition

A variety of teeth were originally examined with respect to the degree of attrition in all animals over six months old; prior to that date the milk teeth are still being replaced by the adult dentition (Markina 1962, Linhart 1968, Haaften 1970). It soon became apparent that the canines, premolars and carnassials were so easily broken that they were of little use in age determination, and as a result only the upper incisors and first upper molars were examined in detail; the lower incisors were worn too rapidly to be of use in age determination. The degree of upper incisor wear was marked on a card showing the outline of the unworn teeth. Molar wear was recorded using the standards of Wood (1958).

4.5.3 Results

Tooth wear proved to be a very variable character, and as such was unreliable as a criterion of absolute age. If an animal showed excessive wear of the incisors, it invariably showed the converse on its molars, and vice versa. Markina (1962) made similar observations; this presumably reflects the animals own food preferences, those with badly worn incisors specialising in biting-types of food, while those with worn molars specialising in gnawing-types of food.

The average degree of incisor wear in winter-killed animals is shown on Figure 11, the lines denoting the amount of wear expected for that year class, up to six years of age. Summer-killed animals show a degree of wear intermediate between the winter samples. There was a large degree of variability in both the degree of development of the various cusps and also the degree of attrition, this often being more pronounced on one side of the mouth than the other, and also was more marked in teeth adjacent to broken or missing teeth. In consequence, any figures given must be an average.

By marking the degree of incisor wear on a blank outline, 65.5% of the animals were aged correctly using the scale in Figure 11, and 93.3% of the sample of animals up to four years of age were aged with only one year error or less (Table 12). With increasing age the amount of additional tooth wear each year was less (Spinage 1973), so that with increasing age the percentage accuracy of this technique diminished (Table 11).

The use of molar wear for age determination was considerably less reliable, showing a greater degree of variability than incisor wear. There was a marked tendency to over-estimate the age of first year winter-killed animals (Table 13), with about half the second and third year animals correctly aged, and thereafter the age was under-estimated. Overall, only 41.4% of the sample was correctly aged, but with one year error or less almost exactly the same accuracy (92.5%) was obtained as with incisor wear (Table 14). Greater accuracy was not obtained if the sample of animals was limited to any one time of the year.

4.5.4 Discussion of Tooth Wear Data

The results obtained here are the converse to those obtained for Urocyon by Wood (1958), in that the incisors show a greater reliability in age determination than do the molars, but even the incisors should only be used as a guide to age. Some animals show an extreme range from

FIGURE 11. AVERAGE ANNUAL ATTRITION OF THE UPPER INCISORS OF WINTER-KILLED SUBURBAN FOXES, UP TO SIX YEARS OF AGE. THE FIGURES REFER TO THE YEAR CLASS.

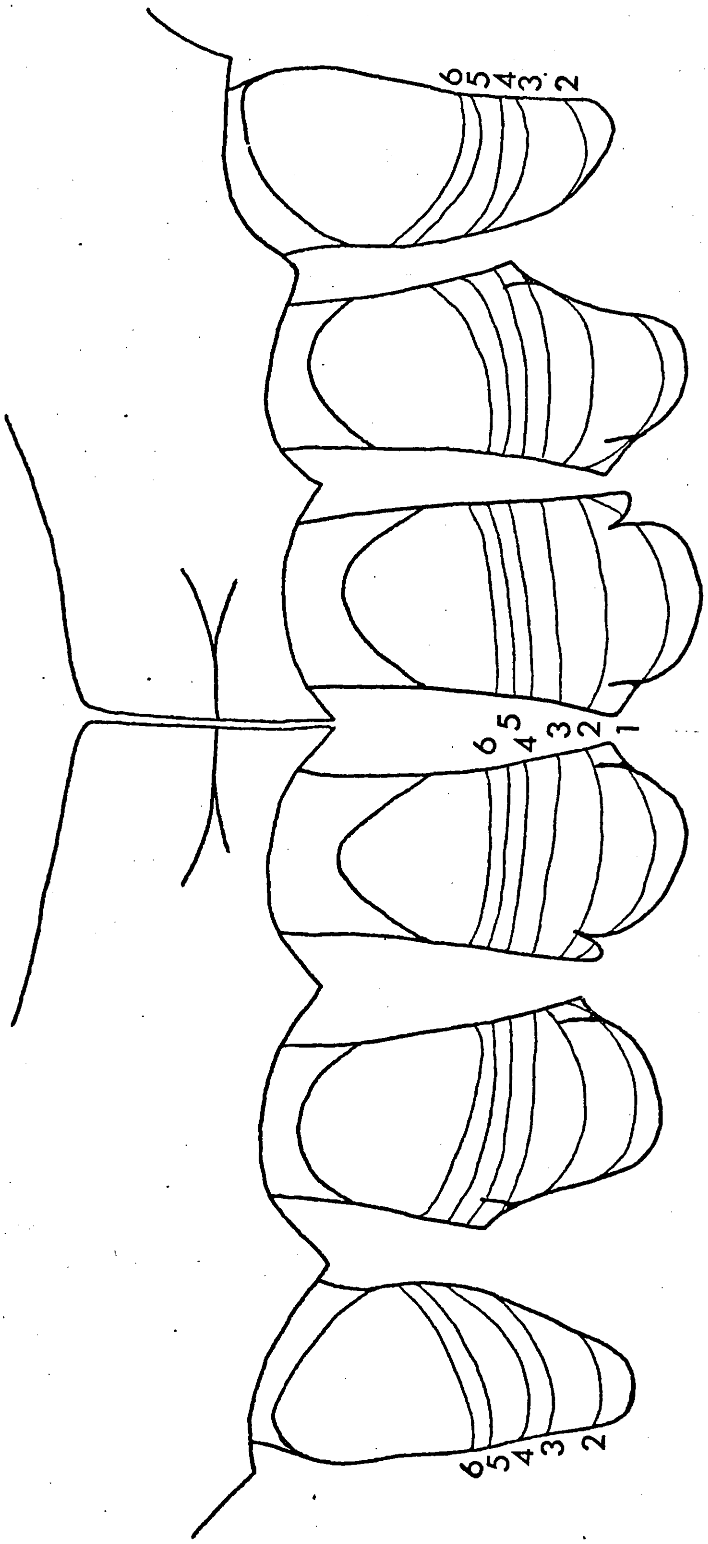

6
5
4
3
2
6
5
4
3
2
1
6
5
4
3
2

TABLE 11

EFFECTIVENESS OF UPPER INCISOR WEAR IN THE DETERMINATION OF AGE IN 165 WINTER (OCTOBER-MARCH) KILLED ANIMALS

		Age estimated from upper incisor wear (Figure 9)									
		1st yr		2nd yr		3rd yr		4th yr		older	
		No	%	No	%	No	%	No	%	No	%
Objective Age	1st year	65	73%	20	23%	3	3%	1	1%		
	2nd year	11	23%	31	65%	4	8%	1	2%	1	2%
	3rd year			6	33%	8	44%	3	17%	1	6%
	4th year			4	40%	1	10%	4	40%	1	10%

TABLE 12

ACCURACY OF AGE DETERMINATION USING INCISOR WEAR IN 165 WINTER-KILLED ANIMALS

	Number	Percentage
Age correctly determined	108	65.5%
1 year error	46	27.8%
2 years error	9	5.5%
3 years error	2	1.2%

TABLE 13

EFFECTIVENESS OF FIRST UPPER MOLAR WEAR IN THE DETERMINATION OF AGE IN 227 ANIMALS SAMPLED THROUGHOUT THE YEAR

	Age estimated from first upper molar wear (from Wood 1958)									
	1st yr		2nd yr		3rd yr		4th yr		older	
Objective Age	No	%	No	%	No	%	No	%	No	%
1st year (October-March)	28	31%	54	60%	6	7%	2	2%		
2nd year	7	8%	47	52%	31	34%	5	6%		
3rd year	1	3%	6	19%	15	47%	10	31%		
4th year			3	20%	7	46%	4	27%	1	7%

TABLE 14

ACCURACY OF AGE DETERMINATION USING FIRST UPPER MOLAR WEAR IN 227 ANIMALS SAMPLED THROUGHOUT THE YEAR

	Number	Percentage
Age correctly determined	94	41.4%
1 year error	116	51.1%
2 years error	15	6.6%
3 years error	2	0.9%

the average, presumably due to individual variations in the calcium content of the teeth, food selection, and other factors.

Incisor wear is most useful in separating the majority of the young of the year from older animals. First year animals show a marked fleur-de-lys pattern to the upper incisors, which are ivory white. This colour and pattern disappear by the second year of life; if the animal shows this fleur-de-lys shape it is a first year animal, while if it does not it could be a first year animal with badly worn teeth but it is more likely to be an older animal. Silver (1969) noted a similar pattern of events occurring in the dog (Canis familiaris), this fleur-de-lys being completely lost by two years of age. Gurskii (1973) claimed that in the wolf (Canis lupus) the first signs of wear do not appear until the fourth to sixth year.

Although both Gier (1968) and Lombaard (1971) have applied this incisor wear technique to Canis latrans and Canis mesomelas respectively, neither have attempted to demonstrate the percent accuracy of their results, and so no comparison can be made with the results presented here.

With the wear on the first upper molar of Urocyon Wood (1958) found a 93.2% accuracy when examining known-age animals. He also noted that there was no difference in the rate of wear between wild and pen-raised animals. Stubbe (1965) did not demonstrate the accuracy of this technique when he applied it to the Red fox, but Bree, Soest & Stroman (1973) found a 35% accuracy with 79 foxes from the Netherlands and 47% of 97 foxes from France. They also noted that most errors did not exceed one year. With 227 suburban foxes over six months of age an accuracy of 41.4% was obtained. This close similarity of the results obtained from foxes sampled in three widely different environments is interesting, especially since one expects a marked variation in tooth wear in relation to the nature of the food.

Despite the tentative suggestion that tooth wear in foxes from different environments may be remarkably similar, tooth wear should not be randomly applied to different populations without reference to known-age material. Even then, it should be used only as a guide to approximate age - Grau, Sanderson & Rogers (1970) with Procyon lotor also noted a high accuracy (82.7%) in aging a sample of animals, but that the overlap was too great to make the method reliable on an individual basis. Exactly the same limitation applies to Vulpes vulpes.

4.6 USE OF CRANIAL SUTURES IN AGE DETERMINATION

4.6.1 Introduction

The rate of closure of the cranial sutures has been used to determine skeletal age in man (Homo sapiens) for many years, each suture being thought to close at a set age, the sequence of closure being rigidly defined, following the standards of Todd & Lyon (1924, 1925a, 1925b, 1925c). Weidenreich (1939), for example, utilised this technique in his study on the duration of life of fossil man in China. However more recent work (Brooks 1955, Genovés 1969) has shown that the process of suture obliteration in Homo sapiens does not follow a well-defined pattern and is an unreliable criterion of age. Genovés (1969) noted that only the basi-sphenoid synchondrosis can be used in age determination, this gap between the basi-sphenoid and basi-occipital being obliterated at about adult hood.

The use of suture closure has been used to determine the age of some wild mammals. For instance, Marks & Erickson (1966) described the sequence of suture closure in the Black bear (Ursus americanus), noting a greater rate of closure in female animals. All sutures were closed in the ninth season in both sexes. Grau, Sanderson & Rogers (1970) found that with the raccoon (Procyon lotor) the closure of the cranial sutures was a continuous process and that the sequence of suture closure allowed separation of male raccoons into seven age groups. There were too few females to allow determination of the sequence of suture closure.

Cranial sutures have been used to determine the age of several canids - Wood (1958) examined the Gray fox (Urocyon cinereoargenteus). He found that most of the skull sutures were closed by January in the first year of the animal's life and he concluded that animals with open or recently closed sutures were 0 - 12 months old.

Dolgov & Rossolimo (1966) described the rate of suture closure in the Arctic fox (Alopex lagopus). They concluded that the external appearance of the skull was of little use for age diagnosis. By a variety of external features, mainly suture closure, they could distinguish first year specimens from individuals of the 1.5 - 2 years and over 2 years age groups. They noted that the basi-occipital and sphenoid suture was closed even in animals only 6 - 10 months old, and in animals 10 - 12 months old the basi- sphenoid and pre-sphenoid suture and a variety of other sutures were ossified. This is a remarkably fast rate of suture closure, only slightly slower than that for the Gray fox (Wood 1958). Dolgov & Rossolimo also noted that age determination in females was still more difficult due to the possibility of considerable error, some female skulls being "infantile" in their characters.

Gurskii (1973) described the sequence of cranial changes with age in the wolf (Canis lupus). He noted that the sutures were obliterated gradually in strict sequence, and that there were no sex differences in the degree of obliteration of the sutures. The sequence of closure was the same as that described for other canids, but the rate of closure was much slower. The basi-occipital synchondrosis begins in animals 7 - 8 months old, being completed in animals 12 - 18 months old. The small suture between the basi-sphenoid and pre-sphenoid started to close in the fourth year, being completed in the sixth year. Similar changes were described for a variety of other sutures.

Churcher (1960) tried to devise a technique for determining the age of the Red fox, using the skulls of 188 known-age farm animals and 1288 wild crania. Using the basi-occipital - basi-sphenoid (BOBS), pre-sphenoid - basi-sphenoid (PSBS) and palatal portion of the pre-maxillar - maxillary sutures (PMMS), alteration in the shape of the post orbital processes (POPS) and of the anterolateral processes of the nasals (ALPN) and texture of the temporal areas (TA), he devised the key included below:-

		Age (months)	Year-class
1.	BOBS open	0 - 9	1st
	BOBS closed -----2.		
2.	PSBS open, TA smooth, ALPN pointed, pulp cavity large	10 - 21	2nd
	PSBS closed, TA roughened, ALPN pointed or bluntly pointed, pulp cavity reduced -----3.		
3.	POPS triangularly pointed	22 - 33	3rd
	POPS spatulately rounded, ALPN usually bluntly rounded -- 4.		
4.	PMMS open	34 - 57	4th + 5th
	PMMS partly fused or fusing	58 - 81	6th + 7th
	PMMS fused	82 +	8th + older

As can be seen, Churcher was of the opinion that the sutures closed in a set order and at precise ages.

Johnston & Beauregard (1969), in their study on rabies epidemiology in Ontario, examined the use of cranial sutures in age determination, also utilising the reference material of 188 known-age crania used by Churcher (1960) in his study. They noted that the suture closure technique "was excellent for distinguishing animals during the first 2 years of life, but there was no way of accurately separating 3 and 4 year old animals by this method. None of the animals showed fusion of the maxillary - premaxillary suture which would indicate an age of 5 years or older". Of the 235 rabid animals that they aged, the oldest was only 51 months, and with such a young sample cranial sutures seemed to be a useful technique, but no attempt was made to correlate this technique with the others Johnston & Beauregard examined.

Markina (1962) also examined the stutures in 166 crania of Russian Red foxes. He found that in animals 6 - 12 months old the basioccipital - basisphenoid suture closed, but since he had no criteria by which to age old skulls he was unable to comment further on suture closure as an age determination technique.

4.6.2 Preparation of Material

Most crania were prepared by allowing the entire corpse to decompose, after which the crania were bleached in a hot solution of sodium perborate. A few crania were defleshed by gentle boiling, and then bleached in the normal way.

The sutures were then scored as open, closing or completely closed.

4.6.3 Results

A variety of sutures were examined with respect to age determination, particularly those sutures used by Churcher (1960) in his key.

Most sutures closed irregularly and proved to be of little use in age determination. The most useful suture was that between the basi-occipital and basi-sphenoid (BOBS). This suture began to close in some cubs as early as June, the first fully closed sutures appearing in cubs in October, and being closed in all animals by January (Table 15). For the three month sample October - December 12/26 (46.2%) did not have the suture fully closed, and so they could still be recognised as young of the year on this character alone. Those with the BOBS suture closed still had the pre-sphenoid/basi-sphenoid suture open or just starting to close and this

TABLE 15

CLOSURE OF THE BASI-OCCIPITAL/BASI-SPHENOID SUTURE IN 108 ANIMALS LESS THAN A YEAR OLD

Month	Open		Closing		Closed	
	No	%	No	%	No	%
May	10	100				
June	17	94.4	1	5.6		
July	7	87.5	1	12.5		
August	8	61.5	5	38.5		
September	2	40	3	60		
October			1	25	3	75
November	1	7.2	8	57.1	5	35.7
December	1	12.5	1	12.5	6	75
January					11	100
February					17	100

character delimited them as first year animals.

The suture between the pre-sphenoid and basi-sphenoid (PSBS) started to close in some animals 7 - 9 months old (Table 16). In the sample taken October - December this suture was closing in 1/28 (3.6%) animals. In the animals 10 - 12 months old (January-March) this suture was closing in 4/61 (6.6%) and was fully closed in 2/61 (3.3%) of the sample, these last two animals being less than a year old. In most animals this suture closed progressively during the second year of life. During the period April - December in the second year of life this suture would characterise second year animals if it was open or closing - if closed the animal could belong to any year class from the second upwards. This allowed recognition of 36/53 (67.9%) of the second year animals up to the end of December. It must be pointed out that in 2/29 (6.9%) of the third year animals this suture remained open, and on this character such animals would be classified as being in their second year.

From January - March of the second year no PSBS sutures were fully open; those animals with the suture closing could equally well be first or possibly third year animals, and those with the suture fully closed could be from the first, second or higher year classes. As already noted, this suture may persist as only partially closed in 6.9% of the third year animals, but sutures that normally closed after the PSBS suture were fully closed in those animals, which enabled their distinction from second year animals.

The rate of closure of the lateral palatal portion of the premaxillar - maxillary suture (PMMS) was even more variable as an indicator of age (Table 17). This suture first started to close in a few animals as they entered the third year class, the first fully closed suture occurring in an animal at the end of that year class. This suture progressively closed during the fourth year (open in 25%, closing in 50%, fully closed in 25%), so that by the fifth year it was either closing (40%) or closed (60%) in all animals. By the sixth year class all PMMS sutures were closed.

TABLE 16

CLOSURE OF THE PRE-SPHENOID/BASI-SPHENOID SUTURE IN 200 ANIMALS

Month		Open		Closing		Closed	
		No	%	No	%	No	%
October		4	100				
November		13	92.8	1	7.2		
December		10	100				
January	First year of life	9	75	2	16.7	1	8.3
February		18	90	1	5	1	5
March		28	96.6	1	3.4		
April		14	93.3	1	6.7		
May		5	45.4	3	27.3	3	27.3
June		4	66.7	2	33.3		
July		1	50	1	50		
August		2	50			2	50
September	Second year of life					1	100
October						2	100
November		1	9.1	1	9.1	9	81.8
December		1	100				
January				3	30	7	70
February				2	15.4	11	84.6
March				1	16.7	5	83.3
April						5	100
May						3	100
June						1	100
July						3	100
August						1	100
September	Third year of life					1	100
October							
November						1	100
December						1	100
January						5	100
February						4	100
March				2	50	2	50

TABLE 17

CLOSURE OF LATERAL PALATAL PORTION OF THE PREMAXILLAR-MAXILLARY SUTURE IN 59 THIRD TO SIXTH YEAR ANIMALS

		Open		Closing		Closed	
		No	%	No	%	No	%
April-June	Third year class	8	88.9	1	11.1		
July-September		4	80	1	20		
October-December		3	100				
January-March		9	64.3	4	28.6	1	7.1
Total for third year class		24	77.4	6	19.4	1	3.2
April-June	Fourth year class	1	25	2	50	1	25
July-September							
October-December				4	80	1	20
January-March		2	66.6			1	33.3
Total for fourth year class		3	25	6	50	3	25
April-June	Fifth year class			1	50	1	50
July-September						1	100
October-December						2	100
January-March				3	60	2	40
Total for fifth year class				4	40	6	60
April-June	Sixth year class					2	100
July-September						1	100
October-December						1	100
January-March						2	100
Total for sixth year class						6	100

No other suture provided even remotely useful data for age determination. Features such as the change in the shape of the post orbital processes, formation of the occipital crests, and formation of the sagittal crest proved to be very irregular, pronounced changes occurring early in the life of some animals, while only faint changes were detected in some quite old animals; although such changes are associated with aging, the rate of change is very variable.

4.6.4 Discussion of Suture Data

The data obtained for the rate of suture closure is of interest since it is at variance with the results of Churcher (1960). As can be seen from the data presented here, the individual rate of suture closure is very variable, with a slight tendency for the rate of closure to be slower in females, although the difference was not marked enough to warrant considering the sexes separately. Dolgov & Rossolimo (1966) noted the same tendency in <u>Alopex lagopus.</u> In a wild population it is completely impossible to assign set ages to the time of suture closure, as did Churcher for his captive-bred animals. The only possible explanation for these widely differing results is that Churchers' animals had been kept and bred under uniform conditions for many generations, and that this tended to eliminate dietary, environmental and genetic factors affecting the time of closure of the sutures, thereby introducing a high degree of uniformity to his sample. This obviously would not be seen in a random collection of wild animals.

The main fault with Churcher's key is that when applied to British foxes it grossly over-estimates age, usually by one year in younger animals, and by three to five years when considering the closure of the PMMS.

Johnston & Beauregard (1969) suggested that this technique "was excellent for distinguishing animals during the first 7 years of life". This was not the case in the present study, the suture technique only allowing recognition of 67.9% of second year animals up to the end of December, and no second year animals thereafter. Also Johnston & Beauregard found that none of their animals showed a fusion of the maxillary - premaxillary suture, although the oldest animal was 51 months old (as aged by cementum lines). This animal was in its fifth year, and in the present study all such animals showed this suture to be closing or fully closed. From the results of Churcher and of Johnston & Beauregard it seems that the rate of suture closure in English foxes is considerably faste presumably due to different ecological, environmental and genetical conditions.

This technique exemplifies the need to check each set of data before applying it to another population.

In all the canids studied, the sequence of suture closure is very similar, although the rate of closure varies considerably. Wood (1958) recorded the fastest rate of closure in Urocyon, followed by Dolgov & Rossolimo (1966) with Alopex. Vulpes is considerably slower than the previous two animals, and Gurskii (1973) recorded a much protracted rate of closure in Canis lupus. In all these animals suture closure allowed the age determination exactly in very young animals, and only approximately in older age classes, since the sequence of closure is fairly (but not invariably) constant.

4.7 USE OF EPIPHYSEAL CLOSURE IN AGE DETERMINATION

4.7.1 Introduction

In theory, the epiphyses of a mammal remain cartilaginous during the period of growth, and become ossified when adult size is attained, so that unfused epiphyses are found in younger animals. According to Morris (1972) not all bones develop at the same rate, so that different epiphyses close in a sequence at differing ages. He also noted that as a rule "epiphyses subject to compression close before those under traction and at a more constant rate".

Morris (1972) reviewed some of the early literature on epiphysis closure, and described his work (Morris 1971) on the epiphyseal fusion of the bones of the forefoot of the hedgehog (Erinaceus europaeus). He recognised seven developmental categories, but the last three categories (animals in their second summer onwards) could not be assigned to a specific age - Morris (1972) noted that in category seven the animals could be anything from 18 months to 5 or 6 years old.

The technique seems to be most useful in separating young of the year from adults e.g. for the Cottontail rabbit (Sylvilagus floridanus) the epiphyseal cartilage of the humerus was used in age determination by Thomsen & Mortensen (1946), the technique being refined by Hale (1949). Lord (1953) utilised the technique to calculate the importance of juvenile animals in the annual cottontail harvest. However when Pelton (1969) compared the epiphyseal closure of the humerus with objective age determined by eye lens weight he found a distinct separation point between presence and absence of the groove in animals approximately ten months old, but the epiphyseal groove was present in some animals twenty months old and absent in some animals only eight months old. Despite the variability of the technique, Pelton concluded that it was still a worthwhile tool for separating most cottontails quickly into two age classes in the field.

Similar studies have been carried out on other lagomorphs e.g. Oryctolagus cuniculus (Watson & Tyndale-Biscoe 1953), Lepus californicus (Tiemeier & Plenert 1964), Lepus europaeus (Walhovd 1966, Cabón-Raczyńska & Raczyński 1972, Pépin 1973), all with very similar results.

There are several other papers utilising the technique to separate young of the year from adult animals e.g. Chipman (1965) for the Cotton rat (Sigmodon hispidus), Sanderson (1961) for the raccoon (Procyon lotor), etc.

Several longitudinal studies of epiphyseal fusion have been made for various breeds of Domestic dog (Canis familiaris) e.g. Seoudi (1948), Pomriaskinsky-Kobozieff & Kobozieff (1954), Bressou, Pomriaskinsky-Kobozieff & Kobozieff (1957), Hare (1959), Smith (1960), Smith & Allcock (1960), Sumner-Smith (1966). These authors considered that sex does not influence the rate of ossification of the epiphyses (unlike rodents and primates), and Smith & Allcock (1960), when comparing the data of several authors, noted that it was surprising that ossification of the epiphyseal cartilages took place at such similar times in various breeds and individuals. All epiphyses were fused by about eighteen months.

Lombaard (1971) studied epiphyseal closure in some of the long bones of Canis mesomelas. He found that the distal epiphyses of the radius and ulna were closing at 40 weeks of age, and fully ossified at 44 weeks; the proximal epiphysis of the radius ossified at 48 weeks; the proximal epiphysis of the humerus was ossified at 48 - 52 weeks. He concluded that X-ray examination of the distal epiphyses of the humerus, radius and ulna allowed distinction between individuals younger or older than eleven months.

Nagretskii (1971) studied the linear growth of the skeleton of the Arctic fox, Alopex lagopus beringensis. He found that the most intense growth of the cerebral part of the skull occurs up to the age of 15 - 20 days, followed by a sharp increase in the relative growth of the facial part, so that by the age of 2 - 3 months the cub skull already has the adult form. Studying the linear growth of the skeletal bones, he found that the greatest absolute gains for all parts of the skeleton were observed in the first three months of post-embryonic life and the least from the age of four to six months. Ossification of the skeleton terminated at the age of four to six months. Growth of the skull ended first, followed by the bones of the peripheral skeleton with the axial skeleton coming last.

Sullivan & Haugen (1956) examined epiphyseal closure in the Red fox (Vulpes fulva = Vulpes vulpes Churcher 1959) and the Gray fox (Urocyon cinereoargenteus). They X-rayed the lower radius and ulna of the forefeet of young captive animals, and found that animals could be classified dependably as young of the year or adults through November, and some were distinguishable through most of December. They took this to indicate that ossification was completed in foxes between eight and nine months of age. A faint and incomplete line along the epiphyseal plate was still visible on some foxes in January, at which time they are approximately ten months old.

Reilly & Curren (1961) examined the proximal epiphyses of the humerus; they showed by means of X-rays that this epiphysis closed at 9 to 9½ months of age, so that for early litters the epiphysis will close in late December, whereas for late litters it will not close until late in January or even February. They suggested that the technique was 100% reliable to the end of November. Reilly & Curren also examined the proximal epiphysis of the tibia and found that the condition of the proximal epiphyses of the humerus and tibia from the same animal in a sample of 238 foxes showed that the status of all categories was similar, so the proximal tibial epiphysis persisted at least as long as the proximal epiphysis of the humerus.

4.7.2 Recording Epiphysis Data

Originally epiphyseal closure was recorded by means of both X-ray plates and by using cleaned bones, prepared by allowing the corpse to decompose and then bleaching the bones in hot (not boiling) 10% sodium perborate. Both techniques yielded the same results, and so for the majority of specimens only cleaned bones were used, although the epiphyses in the feet were always recorded by means of X-ray plates.

The actual age of the cubs was determined in the following way. Eight animals (four males and four females) were raised in captivity, and at weekly intervals the rate of development of the adult dentition was recorded. This confirmed the data of Haaften (1970). The captive animals were X-rayed (and later killed) at set dates to confirm the approximate rate of epiphyseal closure; the rate of tooth erruption was then used to age the cadavers of wild cubs.

4.7.3 Results

For the first three weeks of life no data are available on epiphyseal closure. Thereafter the sequence of epiphyseal closure is shown in Table 18. As can be seen the bones of the feet ossify by 22 weeks of age, those of the vertebral column ossify by 27 weeks, and the limb bones by 30 weeks of age. Thereafter the cartilaginous borders of the scapula, ilium and ischium ossify, and the symphysis pubis and synphysis ischii close, but these processes are gradual and occur at varying rates in different animals, so that an exact time scale cannot be ascribed to their closure.

The time of closure ascribed to each epiphysis is an average, so that a litter of cubs killed in June will show a range of developmental stages, with up to four weeks separating the least and best developed animals in the same litter. As a result epiphyseal closure (and tooth development) are most useful for aging a whole litter of cubs, and with individual animals an error of up to two weeks could occur, this rising to three weeks for a cub killed in the late summer.

After the closure of each epiphysis a line marking the position of the epiphysis was visible on the bone surface for up to four weeks, and can be used to denote recent closure of that epiphysis.

During the autumn and early winter, only one epiphysis is of use for separating young of the year from adult animals, this being the fusion of the apophysis with the diaphysis of the tibia (Table 19). This closes slowly during the autumn, starting to close in October, being fully closed in a few animals killed in November, and in 90% of the first-year animals killed in February. Hence during the autumn and winter an open apophysis denoted a first year animal, but a closed apophysis does not necessarily mean an older animal.

TABLE 18 THE AGES AT WHICH THE EPIPHYSES CLOSE IN RED FOX CUBS

<table>
<tr><th>Approximate Month</th><th colspan="4">April</th><th colspan="5">May</th><th colspan="3">June</th><th></th><th colspan="4">July</th><th colspan="5">August</th><th colspan="4">September</th><th colspan="4">October</th></tr>
<tr><th>Age in Weeks</th><th>1</th><th>2</th><th>3</th><th>4</th><th>5</th><th>6</th><th>7</th><th>8</th><th>9</th><th>10</th><th>11</th><th>12</th><th>13</th><th>14</th><th>15</th><th>16</th><th>17</th><th>18</th><th>19</th><th>20</th><th>21</th><th>22</th><th>23</th><th>24</th><th>25</th><th>26</th><th>27</th><th>28</th><th>29</th><th>30+</th></tr>
<tr><td rowspan="4">Epiphyses of fore and hind feet (carpal and tarsal bones omitted).</td><td rowspan="13" colspan="3">O DATA AVAILABLE FOR FIRST THREE WEEKS OF LIFE</td><td colspan="5"></td><td colspan="3">Epiphysis medial phalanges forefeet</td><td colspan="2"></td><td>Fibular tarsal epiphysis closes</td><td></td><td colspan="3">Epiphysis proximal phalanges forefeet</td><td colspan="12"></td></tr>
<tr><td colspan="6"></td><td colspan="3">Epiphysis medial phalanges hindfeet</td><td colspan="4"></td><td colspan="3">Epiphysis proximal phalanges hindfeet</td><td colspan="11"></td></tr>
<tr><td colspan="15"></td><td colspan="3">Epiphysis metacarpals</td><td colspan="9"></td></tr>
<tr><td colspan="16"></td><td colspan="3">Epiphysis metatarsals</td><td colspan="8"></td></tr>
<tr><td rowspan="5">Epiphyses of vertebral column</td><td>Body cervical 3 - 7</td><td></td><td>Body of axis</td><td></td><td colspan="3">Dorsal arch + ventral plate of atlas</td><td colspan="5"></td><td colspan="3">Odontoid process of axis</td><td colspan="4"></td><td>Cranial epiphysis cervical 6 + 7</td><td>Cranial epiphysis cervical 3 - 5</td><td></td><td colspan="2">Caudal epiphysis of axis</td><td colspan="3"></td></tr>
<tr><td>Body thoracic 12 + 13</td><td></td><td>Body thoracic 1 + 11</td><td colspan="12"></td><td>Cranial epiphysis sacral 1 - 3</td><td colspan="2"></td><td>Caudal epiphysis sacral 1 - 3</td><td>Cranial epiphysis thoracic 1 - 8, 12, 13</td><td>Cranial epiphysis thoracic 9 - 11</td><td></td><td colspan="2">Caudal epiphysis cervical 3 - 7</td><td colspan="3"></td></tr>
<tr><td>Body lumbar 1 - 7</td><td colspan="2"></td><td>Body thoracic 2</td><td>Body thoracic 3, 4, 10</td><td></td><td>Body thoracic 5 - 9</td><td colspan="8"></td><td>Cranial epiphysis coccygeal 1 - 4</td><td>Caudal epiphysis coccygeal 1 - 4</td><td colspan="2"></td><td>Cranial epiphysis lumbar 1 + 7</td><td>Cranial epiphysis lumbar 2 - 6</td><td>Caudal epiphysis lumbar 1 - 6</td><td colspan="2">Caudal epiphysis thoracic 1 - 5, 12, 13</td><td colspan="3"></td></tr>
<tr><td>Body sacral 2 + 3</td><td></td><td>Body sacral 1</td><td></td><td colspan="3">Pars lateralis of sacrum</td><td colspan="9"></td><td>Cranial epiphysis coccygeal 5 - 20</td><td colspan="3"></td><td>Caudal epiphysis lumbar 7</td><td colspan="2"></td><td>Caudal epiphysis thoracic 6 - 11</td><td colspan="3"></td></tr>
<tr><td colspan="20"></td><td>Caudal epiphysis coccygeal 5 - 20</td><td colspan="6"></td></tr>
<tr><td rowspan="4">Epiphyses of limbs and girdles</td><td colspan="2"></td><td colspan="3">Medial epicondyle of humerus fuses to epiphysis</td><td></td><td colspan="2">Tuber scapulae ossifies</td><td colspan="4"></td><td colspan="3">Distal epiphysis humerus</td><td colspan="6"></td><td>Greater trochanter of femur ossifies</td><td colspan="2"></td><td>Distal epiphysis radius + ulna</td><td>Proximal epiphysis humerus</td><td>Cartilage vertebral border of scapula ossifies</td></tr>
<tr><td colspan="2"></td><td colspan="3">Medial malleolus of tibia ossifies</td><td colspan="7"></td><td colspan="3">Medial epicondyle humerus fuses to diaphysis</td><td colspan="4"></td><td colspan="2">Distal epiphysis of tibia</td><td colspan="3"></td><td>Proximal epiphysis femur</td><td></td><td>Iliac + ischiac cartilages of os coxa ossify</td></tr>
<tr><td colspan="4"></td><td>Ischium-pubis ossify</td><td></td><td colspan="3">Os acetabulum, ilium-ischium + ilium - pubis ossify</td><td colspan="3"></td><td colspan="3">Proximal epiphysis ulna</td><td></td><td>Proximal epiphysis radius</td><td colspan="2"></td><td colspan="2">Distal epiphysis of fibula</td><td colspan="2">Distal epiphysis of femur</td><td></td><td>Lesser trochanter of femur ossifies</td><td colspan="2"></td></tr>
<tr><td colspan="12"></td><td colspan="3">Apophysis of tibia fuses to epiphysis</td><td colspan="9"></td><td>Proximal epiphysis tibia + fibula</td><td colspan="2"></td></tr>
</table>

TABLE 19

DATE OF CLOSURE OF THE APOPHYSIS IN 202 ANIMALS LESS THAN 18 MONTHS OLD

	Open		Closing		Closed	
	No	%	No	%	No	%
May	16	100				
June	24	100				
July	4	100				
August	13	100				
September	5	100				
October			5	100		
November			14	87.5	2	12.5
December			6	50	6	50
January			4	36.4	7	63.6
February			2	9.1	20	90.9
March					30	100
April			1	5.3	18	94.7
May					12	100
June					6	100
July					2	100
August					4	100
September					1	100

4.7.4 Discussion of Epiphysis Data

The epiphyses in the Red fox close rapidly, so that most changes are complete by the time the animal is seven months old. The rate of closure is faster than American authors have recorded e.g. Sullivan & Haugen (1956) noted that ossification of the radius and ulna of the fore-feet was complete in foxes eight to nine months old. Similarly Reilly & Curren (1961) examined the proximal epiphysis of the humerus, which they claimed remained open until 9 to 9½ months old, and they suggested that the technique was 100% reliable to the end of November. If this is true for American foxes it certainly is not true for the population studied here, the only epiphysis that remains open beyond seven months of age being the apophysis.

Nagretskii (1971) also noted a fast rate of epiphyseal fusion in the Arctic fox, ossification of the skeleton being terminated at the age of four to six months; the studies differed in that Nagretskii found the bones of the axial skeleton were the last to ossify, whereas in the present study the long bones were the last to ossify completely.

Macintosh (1975) showed that in the dingo (Canis familiaris dingo) epiphyseal fusion occurred earlier than in Domestic dogs, with some epiphyses closing up to seven months earlier in the wild breed of what is assumed to be the same species.

In general it seems that epiphyses close more quickly in wild animals than in domesticated relatives, this presumably being of survival value. The rapid rate of epiphyseal closure in the Red fox renders the technique of little value in determining the age of an adult animal, although it is applicable to animals less than seven months old.

4.8 USE OF GROWTH CURVES IN AGE DETERMINATION

4.8.1 Introduction

Increase in size, either in weight or in linear dimensions, can be used in age determination. It is particularly useful for small mammals which do not live long after adult size is attained. Weight as a measurement is more variable, being directly related to season, reproductive state, fat content and general health of the animal, so that linear measurements are usually more reliable as indicators of age e.g. Brown (1969) studying Apodemus. Flux (1970) gave examples of growth curves for Lepus timidus and found that a lesser degree of variability was found for measurements of hard parts (various bones) than for soft parts (e.g. length of pinna).

A variety of comparatively long-lived mammals have been studied with respect to growth e.g. the raccoon (Procyon lotor) (Sanderson 1961), Cotton rat (Sigmodon hispidus) (Chipman 1965), Fallow deer (Dama dama) (Chaplin & White 1969), etc. and the general conclusion in all studies has been that the age of an animal can be determined only up to the attainment of adult size, usually within a few months, and that thereafter the technique shows little application in age determination.

A variety of canids have been studied in respect of bodily growth. Deavers, Huggins & Smith (1972) studied the growth of beagles in the laboratory. They noted that "some of the numerous factors that influence the growth rate of an organism are the size of the dam, the nutritional state of the dam during pregnancy, litter size, and the availability of food after birth and after weaning. Consequently, even within a particular breed of animal there is a wide range of normal variation in the body weight at birth and during development, which was apparent in the beagles". In the growth curve presented, there was considerable overlap between age classes up to 385 days of age even under their relatively uniform laboratory conditions.

Studies of wild canids have usually shown an even greater variability between age groups in body size. Gier (1968), studying Canis latrans, presented growth curves from birth to maturity (nine months old). He found that sex differences first became evident at 100 to 125 days, and that by 250 days most female weights and measurements fell below the average lines he presented on his graph, and those of the males were above the average. Of the various measurements studied, hind foot and length of head ceased growth earliest, while body length, total length and weight increased for some time longer. Unfortunately Gier made no attempt to show the range of recordings for each age class.

Lombaard (1971) studied Canis mesomelas. He found that measurements for males were larger than those for females, and that cessation of growth occurred at different ages for the various parts of the body measured. Head plus body length levelled out at the age of 40 weeks, hind leg at 22 weeks, ears at 27 weeks, weight and ear-nose length at 32 weeks. Similar results were obtained with various cranial measurements.

Wood (1958) studied growth in Urocyon cinereoargenteus. He found that adult weights were attained by juveniles five to six months after birth, so that weight was of little value in determining age. Weight, with some reservation, could be used to separate age groups in juveniles and juveniles from adults.

Nagretskii (1971) studied the linear growth of the skeleton of Alopex lagopus. He found that the greatest absolute gains of all parts of the skeleton were observed in the first three months of post-embryonic life and the least from the age of four to six months. Growth of the skull ended earliest of all, followed by the bones of the peripheral skeleton with the axial skeleton coming last.

Markina (1962) studied the age craniology of Vulpes vulpes. He applied a variety of measurements to the skull, and developed a variety of indices, but was unable to determine the absolute age of an animal. He divided his sample into four age groups : I (up to 5-6 months); II (6 months to a year); III (1 year to old age); IV (old age). He found that the measurements and indices for groups II, III and IV overlapped, and crania can be divided into these categories on a brief examination without any measuring!

Fairley (1970) studied the growth of cubs from north-east Ireland. He found that the hind foot and pinna of the cubs had effectively reached permanent length by July, but even in September the body weight, body and tail lengths were still increasing, so that even six months after birth foxes are not full grown. However after September it was not possible to distinguish juveniles from adults in autumn on size alone since the largest of the former are as big as the smallest of the latter.

4.8.2 Recording Body and Skeletal Measurements

The recording of body measurements is described in Section 3. Skeletal measurements were made on dried, cleaned bones using a pair of calipers, all measurements being taken to the nearest millimetre.

4.8.3 Results

Growth curves for eviscerated body weight, head plus body length, tail length, hind foot length and pinna length are shown in Figures 12 to 16. As can be seen, growth in foxes is a rapid process, the young of the year reaching adult weight by October/November, maximum head plus body length and tail length by September, maximum hind foot length by July and maximum pinna length in July/August. This reflects the rapid pattern of ossification seen in the skeleton, and so cranial and skeletal measures of growth proved of little value in age determination. Most bones showed a growth pattern very similar to that described for the baculum, and so no more details are included here.

FIGURE 12 GROWTH CURVE FOR INCREASE IN EVISCERATED BODY WEIGHT, SHOWING MEAN, STANDARD ERROR (LOZENGE) AND RANGE OF RECORDINGS. BLACK SYMBOLS ARE DOG FOXES, OPEN SYMBOLS VIXENS.

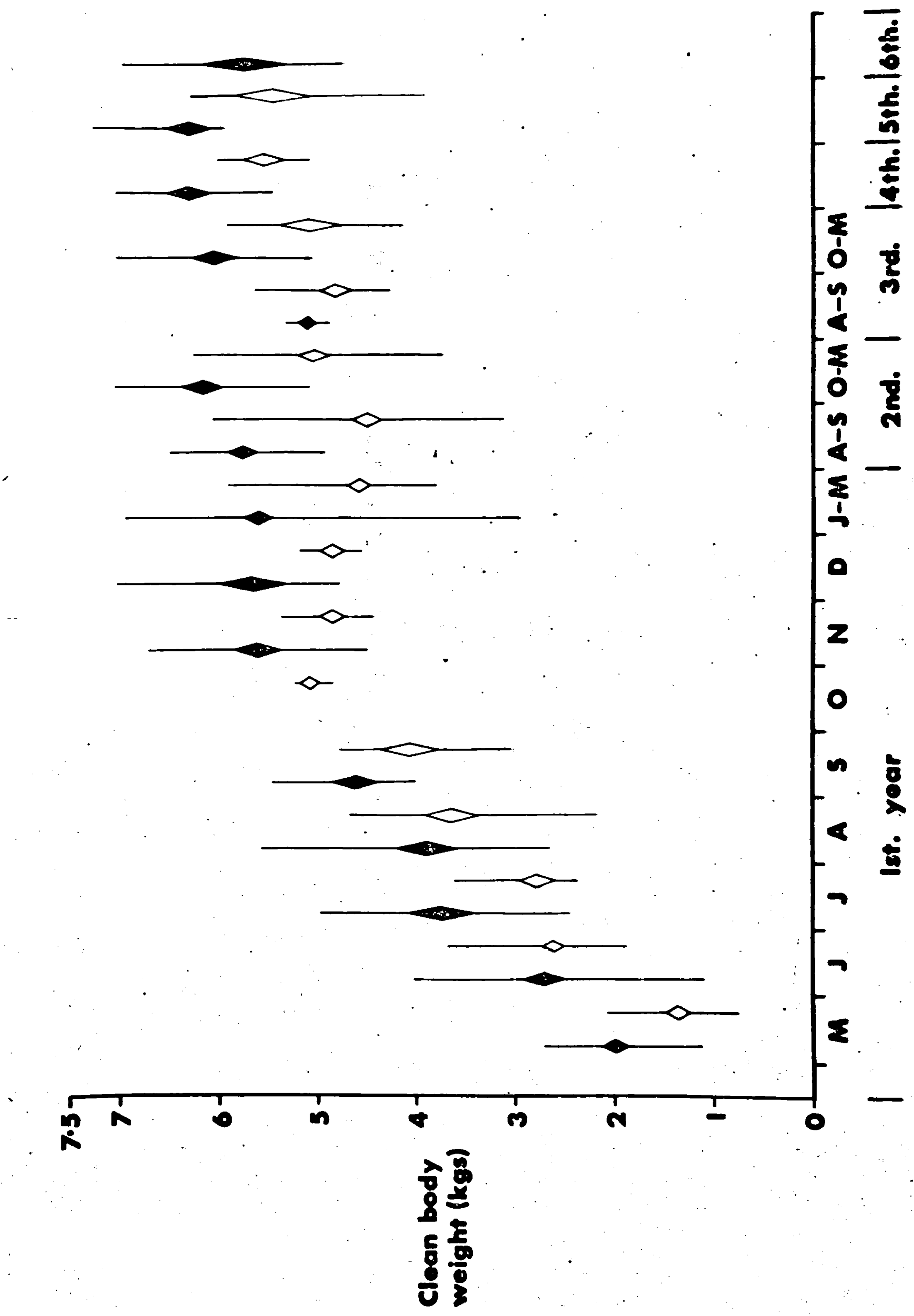

Clean body weight (kgs)
7·5
7
6
5
4
3
2
1
0
M
J
J
A
S
O
N
D
J-M
A-S
O-M
A-S
O-M
1st. year
2nd.
3rd.
4th.
5th.
6th.

FIGURE 13 GROWTH CURVE FOR INCREASE IN LENGTH OF HEAD PLUS BODY, SHOWING MEAN, STANDARD ERROR (LOZENGE) AND RANGE OF RECORDINGS. BLACK SYMBOLS ARE DOG FOXES, OPEN SYMBOLS VIXENS.

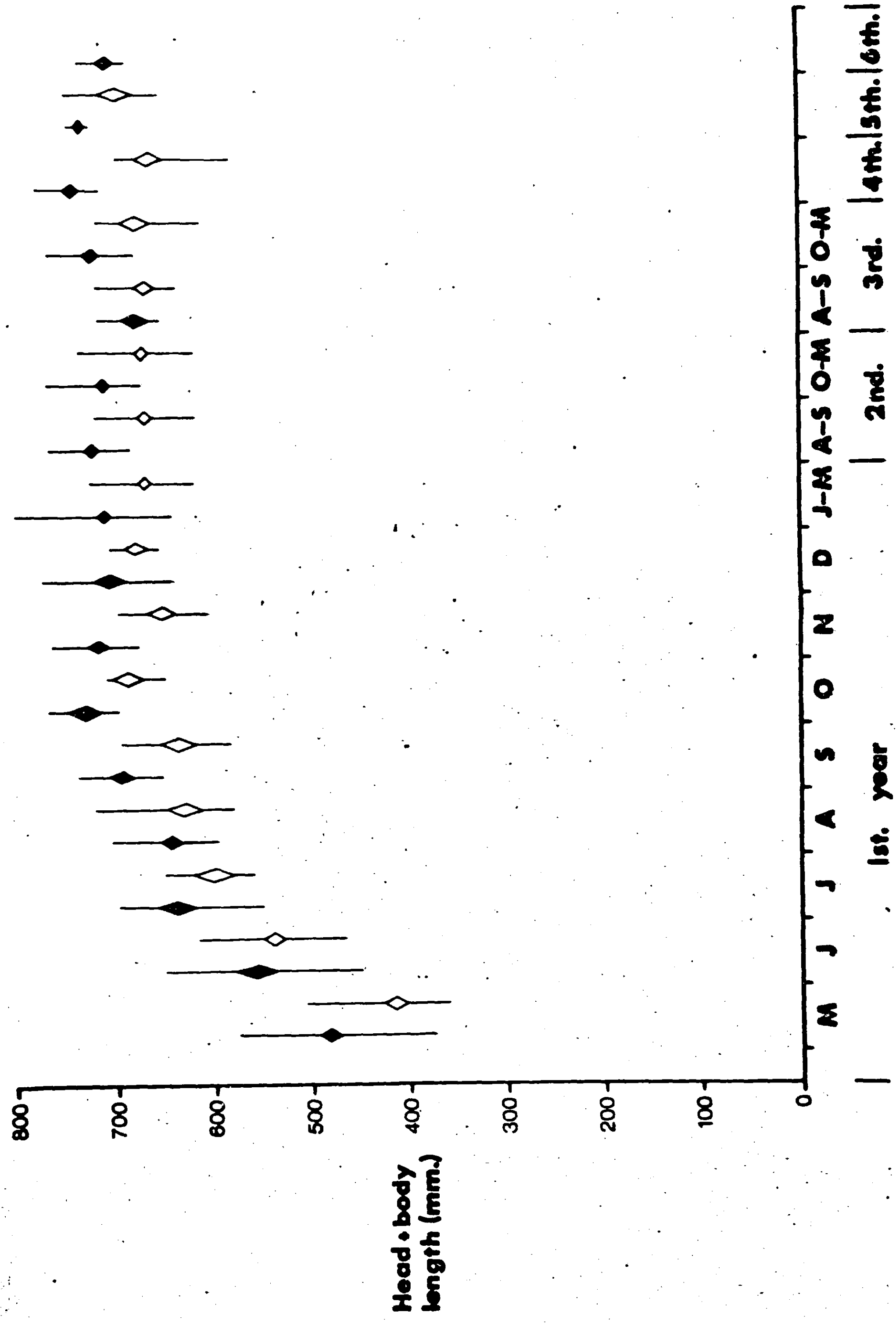

Head + body length (mm.)
800
700
600
500
400
300
200
100
0
M
J
J
A
S
O
N
D
J-M
A-S
O-M
A-S
O-M
1st. year
2nd.
3rd.
4th.
5th.
6th.

FIGURE 14 GROWTH CURVE FOR INCREASE IN LENGTH OF TAIL, SHOWING MEAN, STANDARD ERROR (LOZENGE) AND RANGE OF RECORDINGS. BLACK SYMBOLS ARE DOG FOXES, OPEN SYMBOLS ARE VIXENS.

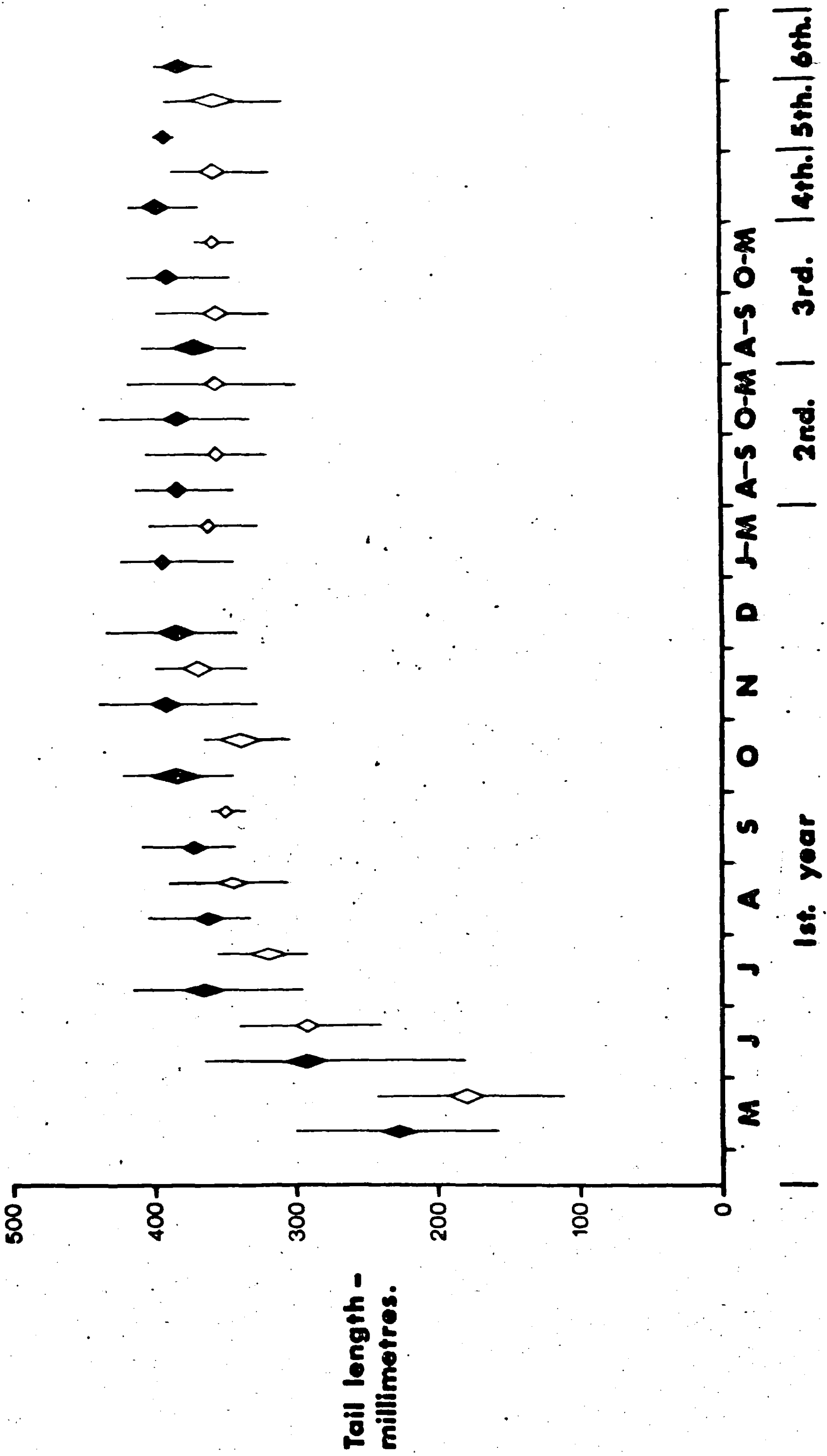

Tail length - millimetres.
500
400
300
200
100
0
M
J
J
A
S
O
N
D
J-M
A-S
O-M
A-S
O-M
1st. year
2nd.
3rd.
4th.
5th.
6th.

FIGURE 15 GROWTH CURVE FOR INCREASE IN LENGTH OF HIND FOOT, SHOWING MEAN, STANDARD ERROR (LOZENGE) AND RANGE OF RECORDINGS. BLACK SYMBOLS ARE DOG FOXES, OPEN SYMBOLS VIXENS.

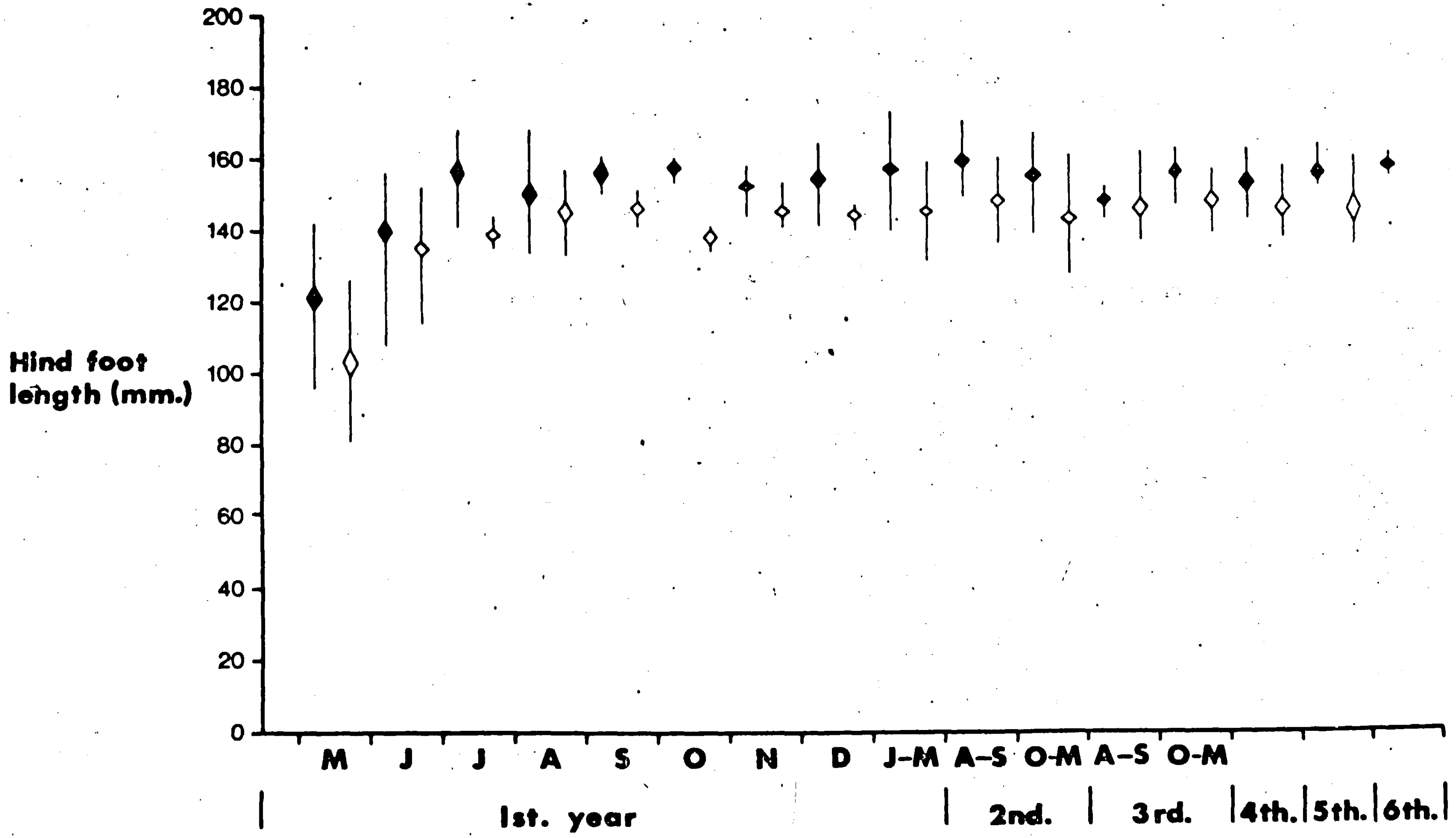
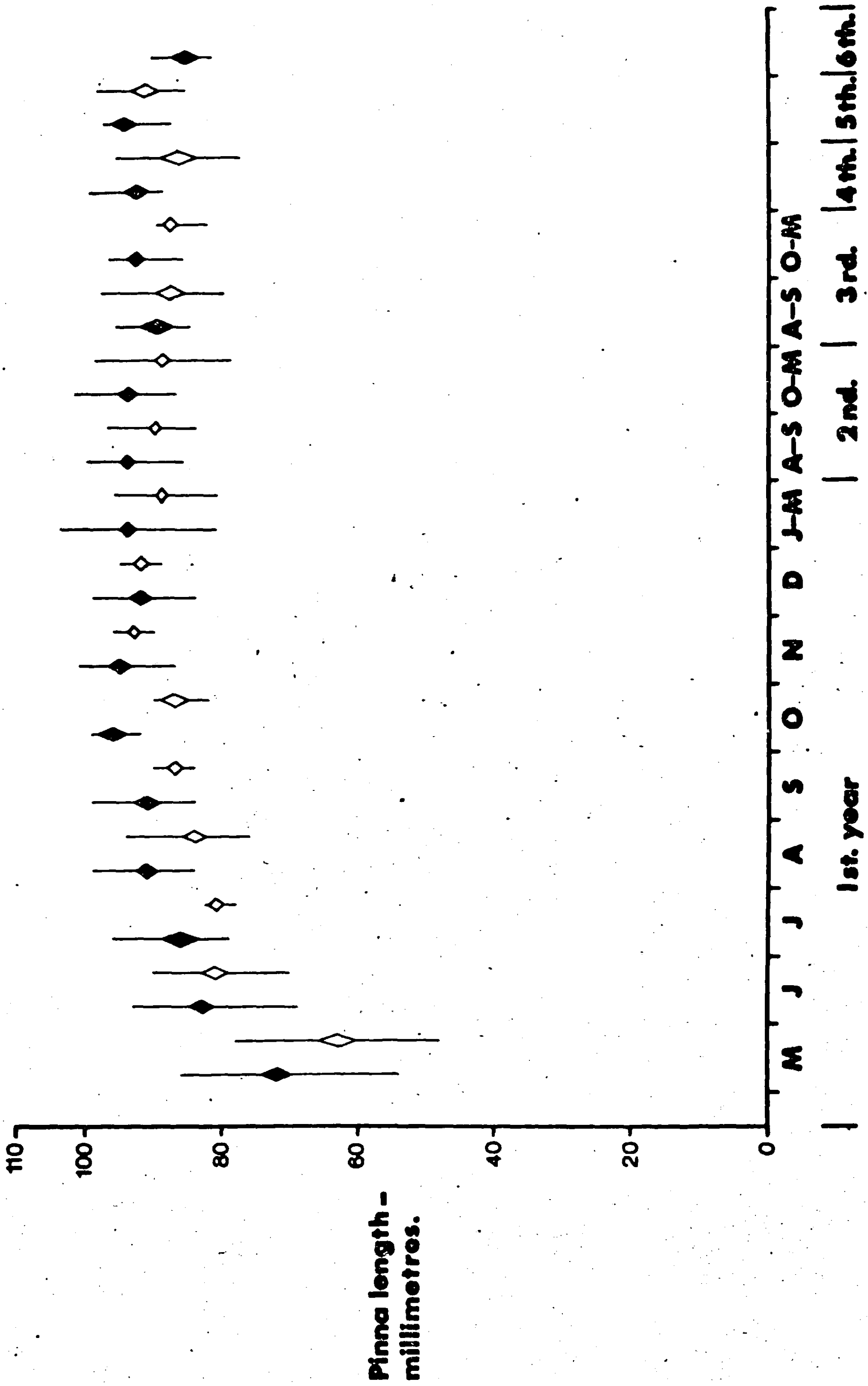

Hind foot length (mm.)
200
180
160
140
120
100
80
60
40
20
0
M
J
J
A
S
O
N
D
J-M
A-S
O-M
A-S
O-M
1st. year
2nd.
3rd.
4th.
5th.
6th.

FIGURE 16 GROWTH CURVE FOR INCREASE IN LENGTH OF PINNA, SHOWING MEAN, STANDARD ERROR (LOZENGE) AND RANGE OF RECORDINGS. BLACK SYMBOLS ARE DOG FOXES, OPEN SYMBOLS VIXENS.


Pinna length - millimetres.
110
100
80
60
40
20
0
M
J
J
A
S
O
N
D
J-M
A-S
O-M
A-S
O-M
1st. year
2nd.
3rd.
4th.
5th.
6th.

4.8.4 Discussion of Growth Data

This rapid rate of growth is typical of wild canids. Fairley (1970) found similar results in Ireland, showing that the hind foot and ear had effectively reached permanent length by July but weight, head plus body and tail lengths continue to increase until the end of September. Lombaard (1971) found similar results for Canis mesomelas, with growth curves all levelling off rapidly by 40 weeks of age (head plus body length levelled out at ±40 weeks, hind leg at ±22 weeks, ear at ±27 weeks and weight at ±32 weeks of age). Gier (1968) found exactly the same growth patterns in Canis latrans, the hind foot and length of head ceasing growth first, while body length, tail length and weight increased for some time longer.

Wild canids all show similar patterns of growth, but the rapid growth rates and the large overlap between age classes renders growth curves of little value in age determination.

4.9 GENERAL DISCUSSION OF AGE DETERMINATION TECHNIQUES

Erickson et al (1970) noted that "In choosing an age-estimation technique .... important considerations are relative accuracy (closeness to actual age), precision (repeatability), and requirements of training, experience, equipment, and facilities".

These criteria are important when considering the value of any individual technique in age determination. Some techniques require skill in interpretation, so that a single skilled recorder should be used to interpret all the data, thereby ensuring uniformity of results. This applies to incisor wear, which often is a subjective estimate due to variables such as the teeth on one side may be badly worn, while those on the other side show little wear, missing teeth produces greater wear on the remaining teeth, and so on. Skill may also be required in the interpretation of tooth sections, although in the present study the annuli were well defined, so that a close correlation was found between the interpretations of an experienced and an inexperienced recorder, suggesting that the technique is repeatable by other workers.

Since virtually all fox litters in London are born one month either side of April 1st, any technique that can separate year classes will give the age of the animal ± one month. Unfortunately only one of the techniques examined (annuli in the cementum of the premolars) was accurate to the nearest year. This technique also has the advantage of being repeatable, and requires relatively little equipment, only requiring some experience in the preparation and interpretation of the sections. The technique can be time-consuming, but once all the material has been collected a large number of sections can be prepared in a short period of time (Allen 1974).

Since the majority of the animals sampled in the winter are young of the year, any technique that can separate all these juveniles during the months October to March is of great value, since it could save a large amount of time spent sectioning teeth that lack annuli in the cementum.

Relatively few of the techniques examined were of value even in this limited respect. The simplest technique considered to be absolutely reliable is to section the canine tooth with a hack-saw; if the pulp cavity is large, about half the width of the tooth, the animal is a juvenile. The only animal that did not conform to this pattern was an adult suffering from a pathological condition of the teeth, but it was easily recognised as a pathological condition and so no error is likely to occur with such animals.

A variety of techniques will separate a proportion of juveniles in the winter sample. These include an open apophysis, an unfused basi-occipital/basi-sphenoid suture in the skull, and a fleur-de-lys pattern to the upper incisors, but these techniques all suffer from a serious drawback in that they cannot be used to recognise all the young animals, and so cannot be used even to calculate the annual recruitment to the adult population.

Similarly Allen (1974) showed that 88% of the juveniles (animals less than a year old) could be separated from the adults by measuring the distance from the enamel line to the alveolar socket of the canine. If, however, the same tooth was cut in half and the size of the pulp cavity examined, all the juvenile animals could be recognised, so Allen's technique holds few advantages.

None of the measures of growth (baculum weight, eye-lens weight, body weight, linear measures of size, skull and skeletal measurements) proved of any value in age determination, not even allowing separation of young of the year from adults in a winter sample. Some measurements, such as baculum weight and eye-lens weight, can be a guide to the approximate age of an adult animal (young, middle-age or old), helping in interpretation of annuli in the tooth cementum. The same applies to incisor wear and suture closure, which allow a broad age grouping of the specimens.

Hence despite claims to the contrary tooth cementum lines, particularly those of the premolars, proved to be the only method for determining absolute age in the Red fox, and the data so obtained has been used in the next section to calculate the age structure and life table of the suburban fox population.

SECTION 5

POPULATION STRUCTURE

5.1 INTRODUCTION

Eberhardt (1969) defined animal population analysis as "the process of attempting to determine the structure (i.e., the age and sex composition) of a population and the forces controlling the past and future composition of that population". Ideally the sample should provide a large number of animals from one area, sampled through a single year, since populations of wild animals are rarely static and fluctuations of numbers are invariably accompanied by changes in structure. The aged sample from suburbia is of limited size (168 males and 168 females) sampled over a two year period. However there was no change in control methods during this period, so it is unlikely that any changes in population structure occurred.

The sample size allows a preliminary analysis of the population structure. More detailed analysis of population dynamics will be deferred until later when a larger sample and more information on reproductive biology, numbers, etc. has been collected.

5.2 DISCUSSION

The ratio of young animals : adults in a sample depends on the intensity of control measures enforced. Most foxes are killed in the winter months. With little or no immigration or emigration, a high effort expended on cub control in the summer yields a winter sample with a low adult to cub ratio - 1 : 1.06 occurs in London (Table 20). (The yearly London sample shows only a slightly higher ratio of 1 adult :

TABLE 20

AGE RATIOS (PROPORTION OF YOUNG ANIMALS IN SAMPLE) IN RED FOX POPULATIONS UNDER DIFFERENT CONTROL REGIMES

Ratio Adults to Juveniles	Author	Locality and Collection Details	Control Regime Where Known
1 : 0.75	Lloyd & Page pers. comm.	Pembrokeshire. 154 foxes collected January to March 1971 & 1972.	
1 : 0.92	Bree, Chanudet, Saint Girons & Stroman 1973.	Netherlands. Data extracted for 48 animals from baculum graph.	
1 : 0.98	Haaften 1970.	Netherlands. Data extracted for 168 animals from eye lens graph.	
1 : 1.06	Petrides 1950.	Ohio, U.S.A. 74♀♀ sampled November 1947 - January 1948.	Open and close seasons; animals harvested for pelts.
1 : 1.06	Present study	London. 192 animals sampled Oct. 1st - Mar. 31st.	Control operations in response to specific complaints. Some natural winter mortality due to mange.
1 : 1.11	Present study.	London. 336 animals sampled through year.	
1 : 2.1	Storm (quoted from Phillips 1970).	Northwest Illinois.	
1 : 2.54	Gier (quoted from Petrides 1950).	Ohio. 85♀ foxes collected October-December 1939-1946.	
1 : 2.60	Phillips 1970.	Northeast Iowa. 203 foxes late October-December 1966 & 1967.	Bounty paid but no intensive control programme.
1 : 2.75	Sullivan & Haugen 1956.	Alabama. 60 foxes trapped at or near dens late summer and fall.	Trapped for bounty in connection with a fox control programme.
1 : 3.02	Jensen & Nielsen 1968.	South Jutland, Denmark. 518 foxes killed mid-October 1967 - mid-January 1968.	Bounty paid since spring 1964, in attempt to reduce fox population to reduce risk of rabies.
1 : 5.6	Phillips 1970.	Central Iowa. 145 foxes late October-December 1966 and 1967.	Intensive control for seven years and a double bounty paid.

1.11 cubs since during the summer many cubs are killed underground by gassing or by terriers and so are never recovered - hence the sample does not represent the true productivity of the population.)

Under intensive control measures e.g. in Denmark where the sample contained a ratio of 1 adult : 3.02 cubs and in central Iowa where the ratio was 1 : 5.60, a very high proportion of the sample was cubs, the number of cubs caught exceeding the natural productivity of the population. Phillips (1970), discussing the Iowa results, noted that intensive trapping yielded few resident foxes, so that many young animals moved into or through the vacant habitat.

The same situation has been noted in other canid species. Knowlton (1967), (quoted from Phillips 1970), studied Canis latrans in southwest Texas. He reported age ratios to be related to the intensity of control effort - 15.7 young/adult being recorded on intensively controlled areas whereas the ratio was only 4.0 young/adult in areas of light control.

More extreme variations in the age ratios are seen in the annual harvest of Alopex lagopus in Russia - Smirnov (1967) recorded a ratio of up to 40 cubs : 1 adult, the high percentage of young animals caught being attributed to the inexperience of that age class. Similarly Macpherson (1969), studying Alopex, found a whelp : adult ratio varying from 100 : 0 to 1 : 100, and he presented a hypothesis to account for this dramatic variation in age ratios. Englund (1970), studying Vulpes vulpes in Sweden, found the proportion of juveniles represented in the samples collected was about 20% too high, the extent of the bias being calculated by comparing the proportion of juveniles in the sample of one year with the proportion of 1½ year old foxes among the adult foxes in the next year. Again this bias was due to the inexperience of the young animals. Where trapping is employed, the sample can be expected to be biased towards inexperienced animals, but in London virtually all the specimens were shot and using Englund's technique no such bias can be detected, although during the winter there is a tendency for the percentage of juveniles in the London sample to fall (Table 21) suggesting early inexperience on the part of the juveniles. However the results are not significantly different at the level P = 0.1 (using a 2 x 2 contingency table). Gier (1968) noted

TABLE 21

AGE DISTRIBUTION OF 192 ANIMALS KILLED OCTOBER 1st. TO MARCH 31st., COMPARING THE CONTRIBUTION OF JUVENILES TO THE EARLY AND LATE SAMPLES

October to December (63 animals):-

Age in Years	0	1	2	3	4	5	6	7
October	7	2				1		
November	16	11	1	2	1	1	1	
December	12	1	3	3	1			
3 month total	35	14	4	5	2	2	1	
Percentage	55.6	22.2	6.3	7.9	3.2	3.2	1.6	

January to March (129 animals):-

Age in Years	0	1	2	3	4	5	6	7
January	12	14	7					
February	22	15	4	2	4	1		
March	30	7	4	3	1	2		1
3 month total	64	36	15	5	5	3		1
Percentage	49.6	27.9	11.6	3.9	3.9	2.3		0.8

X^2 for 1 degree of freedom (using a 2 x 2 contingency table) = 0.578. Difference not significant at P = 0.1 level.

the same trait in Canis latrans populations, although this was not quantified.

Alopex populations are far less stable and such changes in age ratios are very marked in harvested samples (Smirnov 1967, Macpherson 1969). Smirnov (1967) noted that if a disproportionately large number of young animals is caught, the number of young animals in the surviving part of the population is considerably smaller, and the proportion of young animals in the population decreases as the hunting season progresses. Smirnov utilised the nature and extent of these changes to calculate the size of the production stock. Unfortunately his scheme is only applicable to Alopex populations which, due to the close season during their vulnerable breeding period, show a high cub to adult ratio early in the hunting season, followed by significant changes in age ratios as the hunting season progresses.

The absence of a marked autumnal influx of juvenile animals into the sample shows that the London fox population is self-maintaining, any control operations failing to reduce the population below carrying capacity, and the population is not dependent on a regular autumnal influx of new animals. In fact for the winter population (October-March) 516/1000 animals are cubs, the remaining 484 animals being mainly adults in the age range 1 - 5 years (only 1.04% are 6 and 7 year olds and are ignored as an insignificant portion of the population). From the winter life table for adult foxes (Table 25) it can be seen that the average annual rate of adult (1 - 5 years) mortality is 521/1000 adults i.e. an annual loss of 252 adults per 1000 animals in the total winter population. Hence 2.05 cubs are entering the winter population to replace the loss of one adult, and so despite the heavy cub mortality the population is continuing to expand. Presumably some of the surplus is lost by emigration, either further into London (new areas of London are still being colonised) or (presumably) some animals move out of London into the surrounding areas.

The age distribution of 336 animals sampled from London is shown in Table 22, the sexes being treated separately. There is a greater mortality rate for dog foxes in their first year, this being due to their

TABLE 22

COMPARISON OF AGE FREQUENCIES OF SUBURBAN DOG FOXES AND VIXENS

	Dogs		Vixens	
	No.	%	No.	%
0 years	95	56.5	88	48.8
1 year	37	22.0	55	32.7
2 years	17	10.1	15	8.9
3 years	6	3.6	9	5.4
4 years	5	3.0	5	3.0
5 years	6	3.6	2	1.2
6 years	1	0.6		
7 years	1	0.6		
Total	168	100.0	168	100.0

X^2 for 7 degrees of freedom = 9.202

Difference not significant at P = 0.1 level.

greater activity (and hence vulnerability) while dispersing. This is counteracted by a higher mortality rate for vixens in their second year, this being due to their increased vulnerability while rearing cubs. Thereafter the rates of mortality for both sexes are equal, with a slightly greater life expectancy for dog foxes. These differences are not significant at the level P = 0.1. The same trends can be seen in the Danish sample, the two populations being compared on the survival curve (Figure 17). Beck (1973) found the reverse to be true for suburban dogs, the higher rate of mortality occurring in females up to 2 - 3 years of age, and thereafter a higher rate of mortality occurred in males, with a slightly greater life expectancy for females.

The age structure of different fox populations is remarkably similar (Table 23), the greatest deviation being seen in the Danish sample, which was collected from an area subject to intense control activity, whereas the London sample was collected from an area subject to less intense control. In both Danish and London winter samples the age structure of the two sexes is not significantly different (Table 24), and so for further comparison of the two populations the sexes have been combined. For the total sample of each population, the age structures are significantly different (P = 0.001). This difference can be seen on the survival curve (Figure 17), where the Danish population shows a 75.1% cub mortality in the winter, whereas for the London population this is only 51.6%. Thereafter the rate of mortality for each population is constant, as shown by a straight line on the log. survival curve. Calculating the log. regression coefficient for the age range 1 - 5, r = -0.96157 for London dogs, -0.94279 for London vixens, -0.86238 for Danish dogs and -0.98535 for Danish vixens. Similarly the age structure for the two adult populations (animals over one year of age) is not significantly different; the life tables for the winter-killed adults (Table 25) show that for the age range 1 - 5, the average rate of mortality for suburban foxes is 521 adults/1000 adults per annum, and 490 adults/1000 adults per annum for the Danish foxes.

For comparison, provisional life tables have been constructed for London foxes (Table 26) and Danish foxes (Table 27), based on the harvested sample.

TABLE 23

COMPARISON OF AGE FREQUENCIES FOR DIFFERENT RED FOX POPULATIONS, PRESENTED AS PERCENTAGES OF THE TOTAL SAMPLE

Locality	Suburban London			Denmark : South Jutland			Netherlands (1)	Netherlands (2)	Pembrokeshire	Wales
Sex	♂	♀	♂+♀	♂	♀	♂+♀	♂+♀	♂	♂+♀	♀
0 years	56.5	48.8	52.6	77.5	70.9	75.0	49.4	47.9	42.8	59.1
1 year	22.0	32.7	27.4	10.0	13.2	11.2	16.7	33.3	23.4	24.3
2 years	10.1	8.9	9.5	6.1	9.5	7.3	10.7	10.4	13.0	10.0
3 years	3.6	5.4	4.5	3.3	3.2	3.3	6.5	4.2	11.0	4.1
4 years	3.0	3.0	3.0	0.6	1.6	1.0	10.1	4.2	2.6	1.7
5 years	3.6	1.2	2.4	1.5	1.1	1.4	3.6		4.5	0.7
6 years	0.6		0.3	0.9	0.5	0.8	1.2		0.7	
7 years	0.6		0.3				1.2		1.3	
8 years							0.6		0.7	

Source of data:

1.	London :	Present study. 336 animals sampled through the year.
2.	Denmark :	Jensen & Nielsen (1968). 518 animals sampled October 1967 - January 1968.
3.	Netherlands 1:	Haaften (1970). No collection details. Data for 168 animals extracted from eye lens weight table.
4.	Netherlands 2 :	Bree, Chanudet, Saint Girons & Stroman (1973). Data for 48 animals extracted from baculum growth graph.
5.	Pembrokeshire :	Lloyd & Page (pers. comm.). 154 foxes sampled January - March 1971 and 1972.
6.	Wales :	Lloyd (1968). Calculated from annual mortality rate of 61.4% of female population, assuming a constant rate of mortality for each adult age class.

TABLE 24

COMPARISON OF AGE FREQUENCIES IN WINTER SAMPLES OF SUBURBAN AND DANISH FOXES, SEXES BEING CONSIDERED SEPARATELY.

	London			Danish		
	Dogs	Vixens	Total	Dogs	Vixens	Total
0 years	55	44	99	255	134	389
1 year	20	30	50	33	25	58
2 years	12	7	19	20	18	38
3 years	5	5	10	11	6	17
4 years	3	4	7	2	3	5
5 years	3	2	5	5	2	7
6 years	1	0	1	3	1	4
7 years	1	0	1			
Totals	100	92	192	329	189	518

In both samples, the age structure of the sexes are not significantly different.

Comparing the total samples, $X^2 = 44.15$ for 7 degrees of freedom and the difference is significant at the level $P = 0.001$.

Comparing the adult samples (all animals over the age of one year) $X^2 = 6.74$ for 6 degrees of freedom and the difference is not significant at the level $P = 0.1$.

FIGURE 17 SURVIVAL CURVES FOR WINTER-KILLED FOXES FROM LONDON (SUBJECT TO LIGHT CONTROL) AND SOUTH JUTLAND, DENMARK (SUBJECT TO HEAVY CONTROL).

●——●	LONDON	DOGS	AVERAGE AGE 21 MONTHS
○——○	LONDON	VIXENS	AVERAGE AGE 20 MONTHS
■——■	DANISH	DOGS	AVERAGE AGE 15 MONTHS
□——□	DANISH	VIXENS	AVERAGE AGE 16 MONTHS

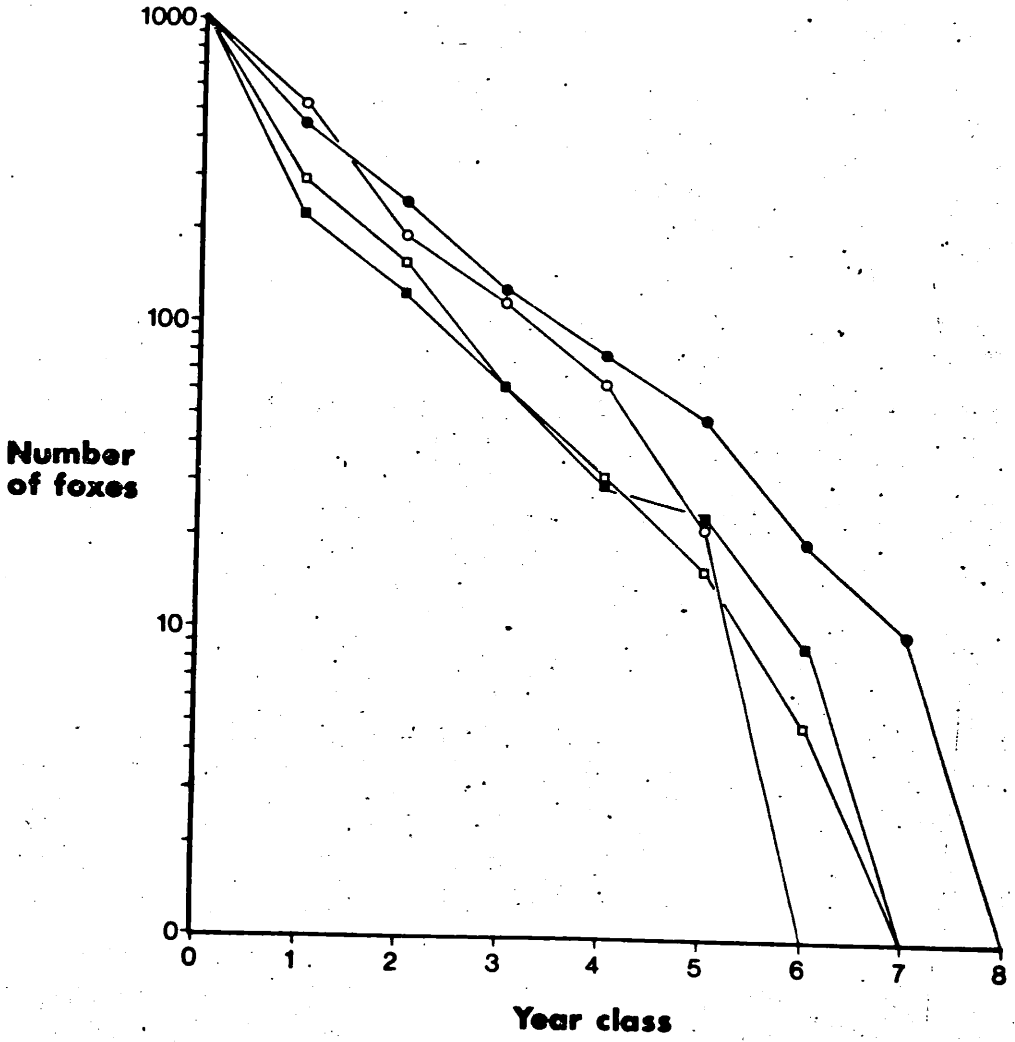

1000
100
10
0
Number of foxes
0
1
2
3
4
5
6
7
8
Year class

TABLE 25

LIFE TABLES FOR WINTER SAMPLES OF SUBURBAN FOXES AND DANISH FOXES (SEXES COMBINED), TO COMPARE ADULT MORTALITY RATES UNDER RELATIVELY LIGHT AND INTENSE CONTROL OPERATIONS

1. Suburban foxes. Average rate of mortality for age groups 1 - 5 521/1000 animals

Age class in years	Number alive at start of year class	Number dying during age class	Mortality rate per 1000 alive at start of age class	Number alive between age x and x+1	Total number of animal age units beyond age x	Expectation of life in years for those attaining age class
x	lx	dx	1000qx	Lx	Tx	ex
1	1000	537	537	732	1484	1.484
2	463	204	441	361	752	1.624
3	259	108	417	205	391	1.510
4	151	75	497	114	186	1.232
5	76	54	711	49	72	0.947
6	22	11	500	17	23	1.045
7	11	11	1000	6	6	0.500

2. Danish foxes. Average rate of mortality for age groups 1 - 5 490/1000 animals.

x	lx	dx	1000qx	Lx	Tx	ex
1	1000	449	449	776	1549	1.549
2	551	295	535	404	773	1.403
3	256	132	516	190	369	1.441
4	124	39	316	105	179	1.444
5	85	54	635	58	74	0.871
6	31	31	1000	16	16	0.500

TABLE 26

LIFE TABLES FOR SUBURBAN FOXES, SEXES BEING TREATED SEPARATELY. SAMPLE COLLECTED OVER A TWO-YEAR PERIOD

1. Dog foxes.

Age class in years	Number alive at start of year class	Number dying during age class	Mortality rate per 1000 alive at start of age class	Number alive between age x and x +1	Total number of animal age units beyond age x	Expectation of life in years for those attaining age class
x	lx	dx	1000qx	Lx	Tx	ex
0	1000	565	565	718	1409	1.409
1	435	220	506	325	691	1.589
2	215	101	470	165	366	1.702
3	114	36	316	96	201	1.763
4	78	30	385	63	105	1.346
5	48	36	750	30	42	0.875
6	12	6	500	9	12	1.000
7	6	6	1000	3	3	0.500

2. Vixens

x	lx	dx	1000qx	Lx	Tx	ex
0	1000	488	488	756	1348	1.348
1	512	327	639	349	592	1.156
2	185	89	481	141	243	1.314
3	96	54	563	69	102	1.063
4	42	30	714	27	33	0.786
5	12	12	1000	6	6	0.500

TABLE 27

LIFE TABLES FOR DANISH FOXES, SEXES BEING TREATED SEPARATELY. DATA CALCULATED FROM JENSEN & NIELSEN 1968. SAMPLE COLLECTED OCTOBER 1967 - JANUARY 1968

1. Dog foxes.

Age class in years	Number alive at start of year class	Number dying during age class	Mortality rate per 1000 alive at start of age class	Number alive between age x and x +1	Total number of animal age units beyond age x	Expectation of life in years for those attaining age class
x	lx	dx	1000qx	Lx	Tx	ex
0	1000	776	776	612	976	0.976
1	224	100	446	174	364	1.625
2	124	61	492	94	190	1.532
3	63	33	524	47	96	1.524
4	30	6	200	27	49	1.633
5	24	15	625	17	22	0.917
6	9	9	1000	5	5	0.500

2. Vixens

x	lx	dx	1000qx	Lx	Tx	ex
0	1000	709	709	646	1069	1.069
1	291	132	454	225	423	1.454
2	159	95	597	112	198	1.245
3	64	32	500	48	86	1.344
4	32	16	500	24	38	1.188
5	16	11	688	11	14	0.875
6	5	5	1000	3	3	0.500

This difference in fox population structure under intense and light control regimes raises several important concepts when considering control operations. Under intense control the effects on the population are:-

a) a reduction in fox numbers

b) the production of a large autumnal influx of juveniles dispersing from areas of higher density, producing a very high cub : adult ratio in a winter sample of foxes.

c) no effect on adult population structure, adult mortality rate or adult life expectancy, the only effect on population structure being to increase the proportion of cubs present.

This increase in the proportion of cubs in a sample is of major importance when considering epizootics. Intense control operations are carried out in areas where rabies is prevalent, but Johnston & Beauregard (1969) have shown that in Ontario in late summer and autumn 66% of the rabid foxes are males, and 65% of the males are juveniles. Heavy control in an area produces a marked influx of the age and sex class most important in spreading the disease. Preliminary data from London suggests that young animals are also most heavily infected with sarcoptic mange, which has recently become a disease of considerable economic importance in London, being readily transmitted from foxes to pet dogs, and in some cases from dogs to their owners.

Any control operations aimed at eliminating either sarcoptic mange or rabies must (a) reduce the numbers of foxes to below a level at which the disease is transmissible and (b) set up a large buffer zone to prevent inward movement of a large number of juvenile (and hence probably infected) animals.

There are a few population studies on other wild canids with which to compare the life tables presented here. Of particular interest is the study on stray suburban dogs in Baltimore (Beck 1973). The life expectancy of the stray animals was less than domestic animals, being 6 - 7 years, the same as in suburban foxes. However, the mean age of Beck's sample was higher (2.31 years for males and 2.62 years for females, compared with 1.41 years for dog foxes and 1.35 years for vixens in suburban London). Beck accounted for 23% mortality a year and estimated that it could be as high as 50%, with a minimum of 44.9% of the population dying in its first year. This is a remarkable parallel to the London results, and the two populations, occupying similar ecological niches, are subject to the same level of predation.

Macpherson (1969) presented a life table for Canadian Arctic foxes, which showed a much higher mortality rate, only 39.1% of the population reaching six months of age, and very few, if any, of the animals exceeding 4½ years of age.

Similarly Wood (1958) found a higher rate of mortality for the Gray fox; he also found no difference in mortality rates between males and females. The mortality rate between the first and second November of life being 70%, and thereafter 50% per annum. 50% of the cubs died in their first summer, 90% in their first winter. Only 9% of his population was two years of age and over.

Mech (1970) compounded survival curves for the wolf (*Canis lupus*) in North America, the data being drawn from several sources. He suggested a maximum life span of 10 - 11 years, with a 50% annual adult mortality under moderate to heavy exploitation, and 22% annual adult mortality in unexploited populations (presumably this was due to natural causes). Knowlton (1972) presented a proposed model of the annual cycle of coyote numbers under unexploited and intense control regimes; this showed the same population trends as Mech described for the wolf. Mech (1970) also reviewed the literature on pup : adult ratios in wolf populations before and after control operations. The results showed a marked increase in the proportion of cubs in populations under intense control operations, so paralleling the results for fox populations, although here the increase in the proportion of cubs is due to increased productivity rather than by immigration as in fox populations.

Thus the derived structure for the London fox population shows that the population is subject to limited control measures, is self-maintaining, with twice as many cubs entering the winter population as adults being killed each year. The structure of the population is very similar to other Red fox populations subject to normal levels of control, and these populations only differ in structure from populations subject to intense control in the ratio of cubs to adults sampled during the winter months, the rate of annual adult mortality remaining constant. This contrasted with the population data collected for the wolf, where the rate of annual adult mortality was doubled in populations subject to intense control.

SECTION 6

SPONDYLOSIS DEFORMANS IN THE RED FOX

6.1 INTRODUCTION

Of the various diseases, injuries and pathological conditions that affect suburban foxes, spondylosis deformans was selected for detailed study since the condition is easily quantified. Spondylosis deformans is a condition of the spinal column, and is characterised by the formation of bony spurs and bridges across the intervertebral spaces (Figures 20 and 21).

The early literature concerning the condition, especially that referring to man, is largely confused and contradictory. Spondylosis is frequently found in man as a consequence of a radiological examination of an unrelated complaint, but few papers agree as to the pathological nature, frequency, distribution and clinical significance of the condition. This lack of agreement has led to the use of several terms to describe the same condition. A review of the terminology is presented by Morgan (1967), Morgan, Ljunggren & Read (1967) and Read & Smith (1968), who suggest the use of the term "spondylosis deformans" to describe the condition of osteophytes of the vertebral body, and "spondylosis ankylopoetica" for the condition of osteophytes of the synovial joints of the vertebral column. This terminology will be adhered to here.

Morgan (1967), in his monograph on spondylosis in the dog, presented valuable histological, clinical and experimental data, in addition to his morphological work (Morgan also gave a full review and discussion of the earlier work in those fields, and since no histological, clinical or experimental data are presented here, only current ideas are expressed. For a full review of the literature in these fields see Morgan (1967)). Morgan showed that the structure of the osteophytes did not differ from that of the vertebral bodies and that the osteophytes eventually became an integral part of the vertebrae. The intervertebral discs have for long been suspected to be of importance in the pathogenesis of spondylosis - Morgan showed that changes within the anulus fibrosus of the disc led to intradiscal fissures that predisposed the formation of the osteophytes. Morgan also showed that no correlation existed between clinical signs and spondylosis deformans.

Although detailed examination of the condition has only been completed for dogs and cats, spondylosis deformans has been reported from the following groups of domestic animals : bovines (Frank 1939, Anon.1956/7, Bane & Hansen 1962, Jubb & Kennedy 1963, Stecher 1963), camels (Hansen & Mostafa 1958), cats (Glenney 1956, Beadman, Smith & King 1964, Read & Smith 1968), dogs (Hansen 1952, Glenney 1956, Archibald & Cawley 1966, Morgan 1967, Morgan, Ljunggren & Read 1967, Read & Smith 1968, Bellars & Godsal 1969, Harcourt 1971), equines (Callender & Kelser 1938, Stecher & Goss 1961), sheep (Harcourt 1971), and swine (Feldman & Olson 1933, Jubb & Kennedy 1963, Harcourt 1971).

For species of wild mammals, reports of spondylosis deformans are scattered. Moodie (1923) showed the antiquity of the condition, the earliest fossils in which these osteophytes have been recorded are dinosaurs of the Comanchean period 110 million years ago. Moodie also documented a continuous fossil history for the condition, with reports of osteophytes in Cretaceous dinosaurs, primitive Eocene ungulates, an Egyptian crocodile from the Miocene, a Pliocene camel, and cave-bears and saber-tooth cats of the Pleistocene. In the same vein Moodie presents examples from earlier human races - Neolithic man, ancient Egyptians, and pre-Columbian Indians of America.

In his survey of diseases in captive wild mammals Fox (1923) makes no mention of spondylosis, but in his monograph on chronic arthritis in mammals Fox (1939) presents many examples. In total Fox examined 1,749 skeletons, of which 77 showed some form of arthritis. Fox's material was derived from both wild and menagerie sources, and this sample represented most of the major groups of mammals. Fox demonstrated spondylosis to be present in Marsupialia, Artiodactyla, Perissodactyla, Carnivora (families Ursidae, Hyaenidae, Viverridae and Felidae) and Primates. However, throughout his survey Fox stresses the absence of any form of arthritis in the family Canidae.

In addition to the observations of Fox (1939) spondylosis deformans has been reported from the following groups of wild mammals : Ursidae (Stecher 1963), Cetacea (Crisp 1860, Slijper 1936, Bree & Nijssen 1964), Primates (Stecher 1958), and Cervidae (Chapman & Chapman 1969a). The frequent pathologists' reports from the larger zoological collections also contain frequent references to spondylosis in menagerie specimens, but detailed reference to these reports is not included since the specimens referred to are living under artificial conditions, and are often of an unusually advanced age. These reports do not refer to any canids or other groups not already mentioned as exhibiting spondylosis.

Although Fox (1939) was mistaken in stating that wild Canidae do not exhibit arthritis, there are only a few reported cases of spondylosis in this family. Merriam (1912) reported spondylosis in the large extinct wolf Aenocyon dirus Leidy from the tar pits of Rancho la Brea in Southern California. Cross (1940) recorded spondylosis in the spine of a wild male Timber wolf (Canis lupus lycaon). Gadzhiev & Gadzhiev (1954) described spondylosis deformans in vertebrae of various skeletons of the Binagadinsk wolf (Canis lupus apsheronicus) from the Quarternary Era, and as a result of their findings pointed out the need for a comprehensive study of this condition in contemporary mammals.

The occurrence of spondylosis in the large canids is not surprising. Hamerton (1944) noted ankylosis of the coccygeal vertebrae of a specimen of Nyctereutes procyonoides in London Zoo as a result of an injury, but it is unclear as to whether this was due to spondylosis deformans or to some other condition. Spondylosis deformans has not previously been confirmed in any of the smaller wild canids.

6.2 COLLECTION AND PREPARATION OF MATERIAL

The skeletons of all foxes were prepared by allowing the entire carcass to decompose in the open air. Any remaining muscles and ligaments were then removed by gentle boiling, and the bones were finally bleached in a hot 2.5% solution of sodium perborate (Chapman & Chapman 1969b).

Only skeletons with all vertebral epiphyses fused were used. This gave a total of 252 usable vertebral columns (122 males and 130 females). Unfortunately it was common practice by the suppliers to remove the "brushes" of the foxes killed, and this was done either by skinning the tail (when a variable number of terminal vertebrae were often lost) or by cutting off the entire tail (when all except the four proximal caudal vertebrae were lost). As a result a number of specimens have some or all tail vertebrae missing.

6.3 RECORDING OF OSTEOPHYTES

Skeletal anomalies can be recorded by means of radiographs, anatomical studies, or clinical studies. The latter are not possible with a wild population. Although radiographs are both quicker and simpler, more accurate results can be obtained from anatomical studies. Schmorl & Junghanns (1959) noted that anatomical studies show a far higher incidence of spondylosis than do clinical and radiological studies. Similarly Beadman, Smith & King (1964) noted that only 85% of the osteophytes found in post-mortem examinations were visible on routine lateral radiographs. Morgan, Ljunggren & Read (1967) found that a higher incidence of spondylosis was recorded when the spine was removed before X-raying, thereby increasing the efficiency in locating osteophytes.

However, these workers still found that identification of small lateral osteophytes was almost impossible, and it was also felt that most dorsal or dorsolateral osteophytes were missed because of their small size and the presence of overlying structures. In view of the difficulties outlined, only cleaned material was used in the present study.

The cleaned vertebrae were examined macroscopically for osteophytes, using a x10 hand lens when necessary. Each vertebral margin was divided into four segments (dorsal, ventral, left and right lateral) as described by Morgan (1967), and on each segment the osteophytes were classified by size, using the standards of Nathan (1962). Thus stage one consisted of the smallest osteophytes on the vertebral margins; in stage two larger osteophytes were seen but these did not project beyond the vertebral end plate; in stage three the osteophytes projected beyond the vertebral end plate but opposing osteophytes did not fuse; in stage four actual fusion between opposing osteophytes occurred (Figures 18 and 21). Where more than one osteophyte was present on each segment only the largest was recorded.

Similar size standards were used by Morgan (1967) to measure the osteophytes on dog vertebral columns. However Morgan used five standards, stages two to five being exactly the same as stages one to four of Nathan (1962) and the present study. Stage one in Morgan's study consisted of soft tissue only (described as palpable nodules), which is only recognisable in dissected specimens and hence cannot be recorded from cleaned vertebrae or from macroradiographs.

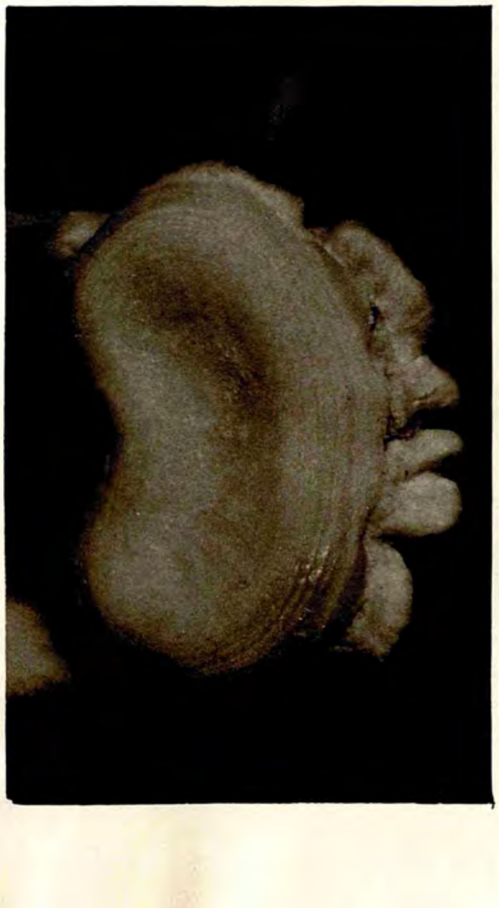
It is necessary to have some method of comparing the degree of affection between animals, and for this purpose an Affection Index was devised. This was obtained by summating the sizes of the largest osteophytes recorded on each segment of each vertebral margin, thereby giving a total "Affection Index" for each animal. Since many specimens have some caudal vertebrae missing the Affection Indices presented here were based only on the cervical, thoracic, lumbar and sacral vertebrae.

FIGURE 18 STAGES IN THE DEVELOPMENT OF AN OSTEOPHYTE ON THE VERTEBRAL MARGIN

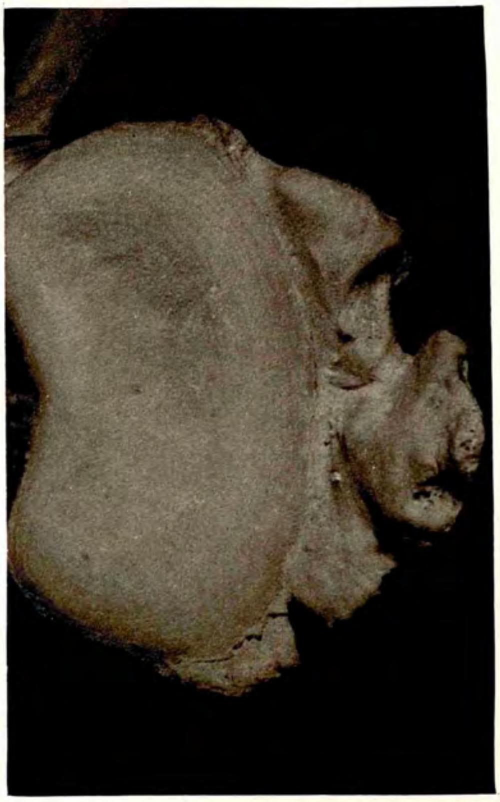
a. NO OSTEOPHYTES
b. STAGE 1 OSTEOPHYTE
c. STAGE 2 OSTEOPHYTE
d. STAGE 3 OSTEOPHYTE

a.

b.



c.

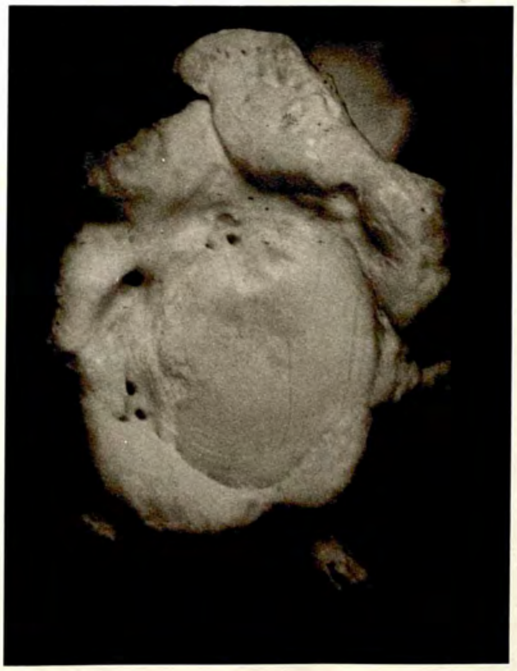


d.

FIGURE 19 SPONDYLOSIS DEFORMANS

a. CAUDAL VERTEBRA, SHOWING THE DEVELOPMENT OF OSTEOPHYTES ON ALL FOUR QUARTERS OF THE VERTEBRAL MARGIN

b. THORACIC VERTEBRA, SHOWING OSTEOPHYTES DEVELOPED AROUND THE COSTAL ARTICULATIONS



a.

b.

FIGURE 20 SPONDYLOSIS DEFORMANS ON THORACIC VERTEBRAE 1 - 10 OF NO. 1014, SHOWING OSTEOPHYTES PARTICULARLY WELL DEVELOPED ON THORACIC 3 AND 4.

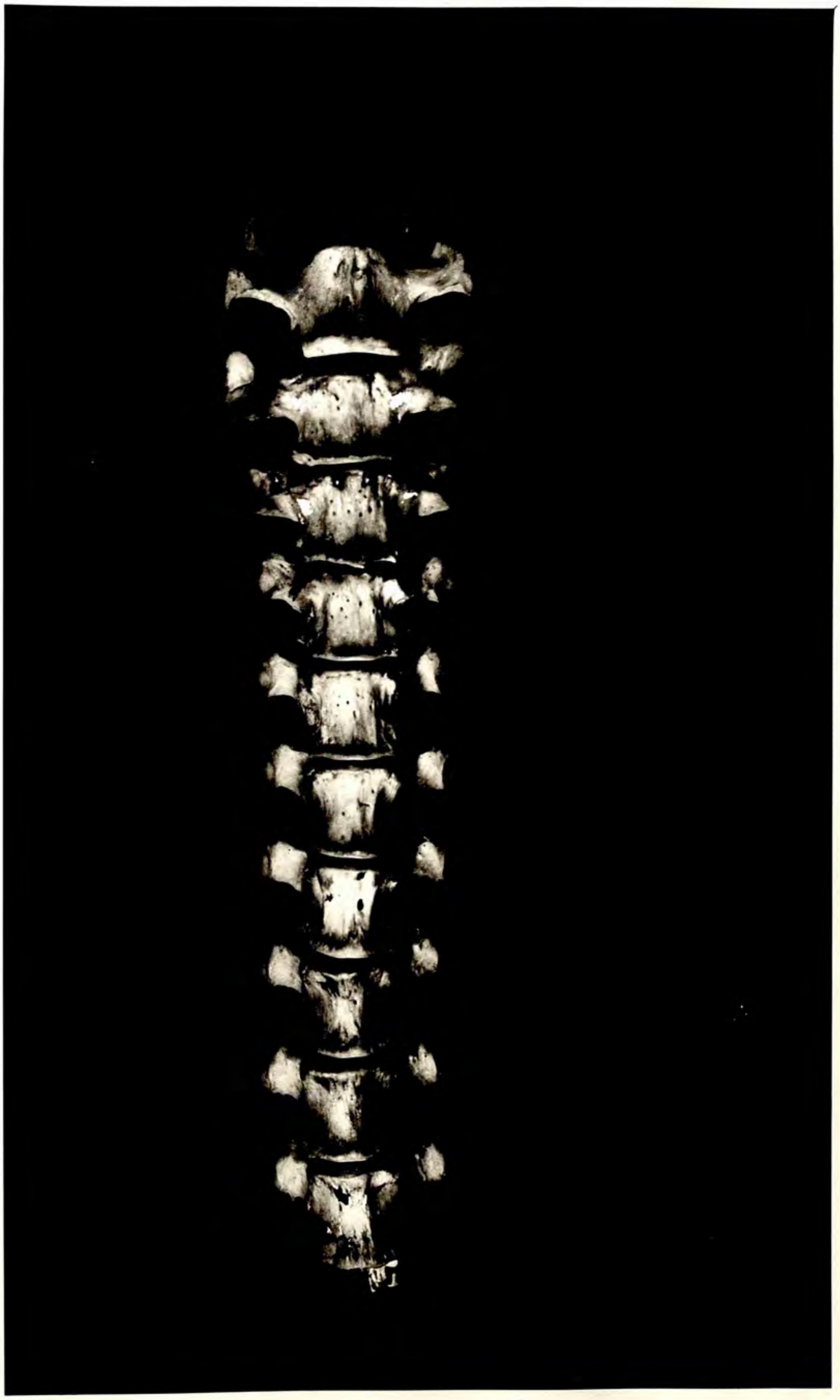


FIGURE 21 SPONDYLOSIS DEFORMANS ON LUMBAR VERTEBRAE OF NO. 1028. GRADE 4 OSTEOPHYTES ARE SEEN FUSING LUMBAR 4 AND 5.

The intervertebral discs are numbered according to the system of Hansen (1952).

6.4 RESULTS

6.4.1 Number of Animals Affected

34.5% of the total sample was affected with spondylosis with a slightly higher percentage of the males affected. However this difference was not significant at the level P = 0.1 (Table 28).

6.4.2 Degree of Affection

The degree of affection (Affection Index) is shown in Table 29 and Figure 22. Although the proportion of males and females affected was not significantly different, the Affection Index of the affected males was significantly higher than that for affected females at the level P = 0.05.

6.4.3 Distribution of Osteophytes along the Vertebral Column

In the pre-sacral vertebrae peaks of affection are seen at the cervico-thoracic and lumbo-sacral junctions (Figure 23). The greatest number of affected discs occurs at the cervico-thoracic junction, but a higher Affection Index is found at the lumbo-sacral junction (Figure 24). Minor peaks are seen at discs 8 and 9 (thoracic vertebrae 2 to 4), disc 20 (lumbar vertebrae 1 and 2), and discs 24 and 25 (lumbar 6 and 7). Very low levels of affection are seen in the cervical and mid-thoracic regions.

In the post-sacral vertebrae the pattern of distribution is reversed. The peak of affection is seen in the mid-caudal region, diminishing towards each end of the tail. The first four caudal vertebrae are morphologically distinct from the rest of the caudal vertebrae and they show a markedly lower incidence of spondylosis.

TABLE 28

NUMBER OF ANIMALS AFFECTED WITH SPONDYLOSIS DEFORMANS

	Total Sample		Males		Females	
	No	%	No	%	No	%
Affected	87	34.5	45	36.9	42	32.3
Unaffected	165	65.5	77	63.1	88	68.7
Total	252	100.0	122	100.0	130	100.0

Comparing the numbers of males and females affected, $X^2 = 0.591$ for 1 degree of freedom. Difference is not significant at the level $P = 0.1$.

TABLE 29

DEGREE OF AFFECTION WITH SPONDYLOSIS DEFORMANS

Affection Index	Total Sample		Males		Females	
	No	%	No	%	No	%
0	165	65.48	77	63.11	88	67.70
1-10	49	19.44	18	14.75	31	23.85
11-20	15	5.95	10	8.20	5	3.85
21-30	8	3.17	4	3.28	4	3.08
31-40	2	0.79	2	1.64	-	-
41-50	5	1.98	4	3.28	1	0.77
51-60	4	1.59	3	2.46	1	0.77
61-70	-	-	-	-	-	-
71-80	1	0.40	1	0.82	-	-
81-90	1	0.40	1	0.82	-	-
91-100	-	-	-	-	-	-
101-110	1	0.40	1	0.82	-	-
111-120	-	-	-	-	-	-
121-130	-	-	-	-	-	-
131-140	-	-	-	-	-	-
141-150	-	-	-	-	-	-
151-160	1	0.40	1	0.82	-	-
Total	252	100.00	122	100.00	130	100.02

Comparing the degree of affection in males and females, $X^2 = 13.08$ for 6 degrees of freedom. Difference was significant at the level $P = 0.05$.

FIGURE 22 HISTOGRAM SHOWING DISTRIBUTION OF AFFECTION INDEX FOR SPONDYLOSIS DEFORMANS

▩ MALES
▨ FEMALES

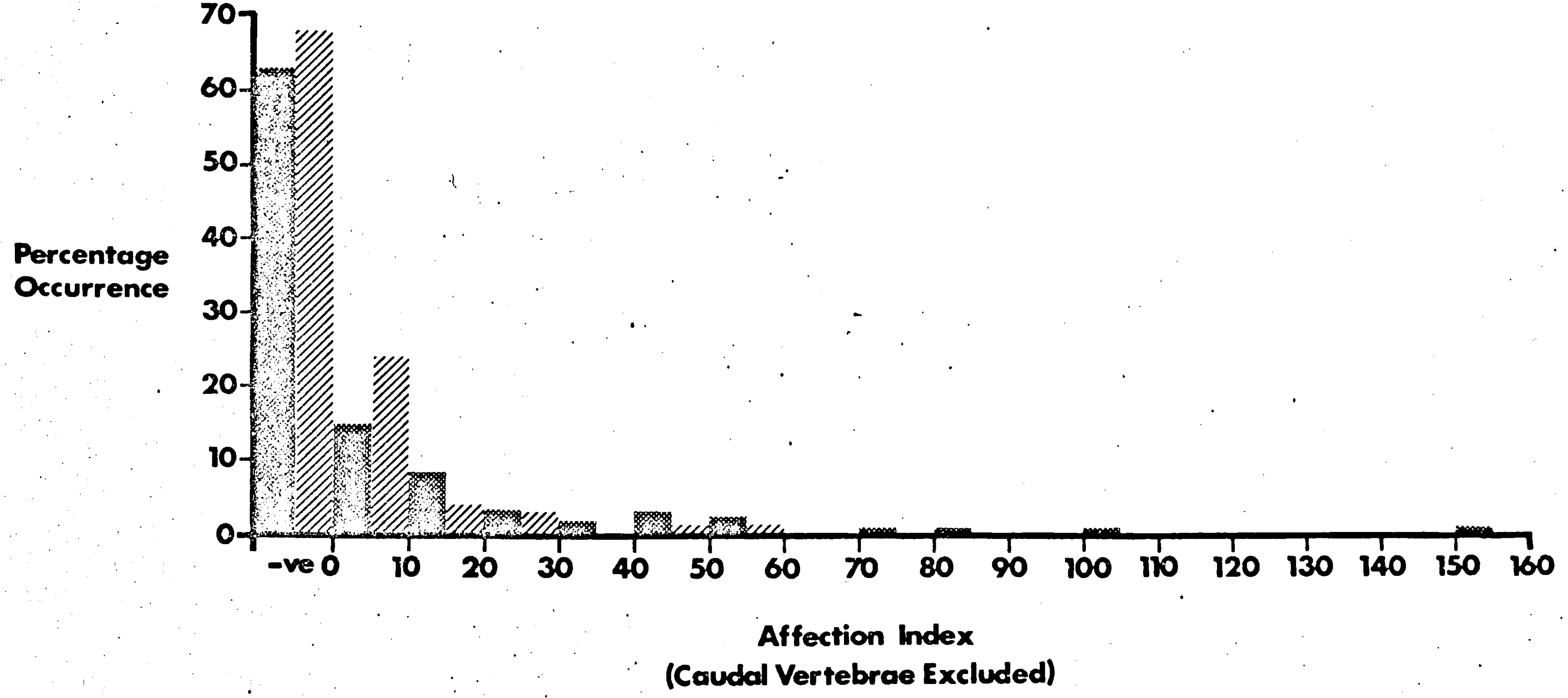

Percentage Occurrence
70
60
50
40
30
20
10
0
-ve 0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
Affection Index
(Caudal Vertebrae Excluded)

FIGURE 23 FREQUENCY DISTRIBUTION OF SPONDYLOSIS DEFORMANS, SHOWING PATTERN OF DISTRIBUTION ALONG THE VERTEBRAL COLUMN

●——● ANTERIOR EDGE OF DISC SPACE

○- - -○ POSTERIOR EDGE OF DISC SPACE

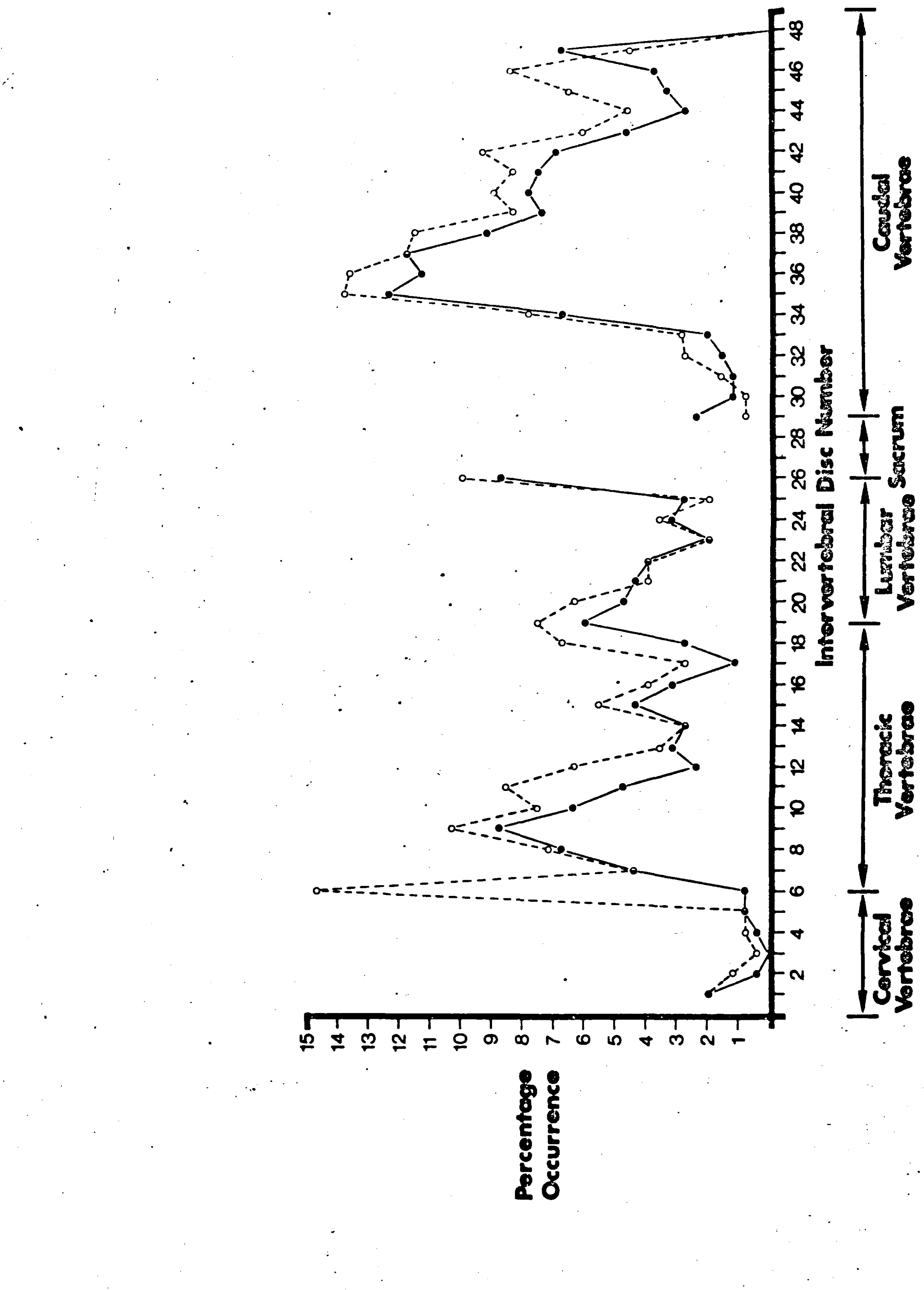
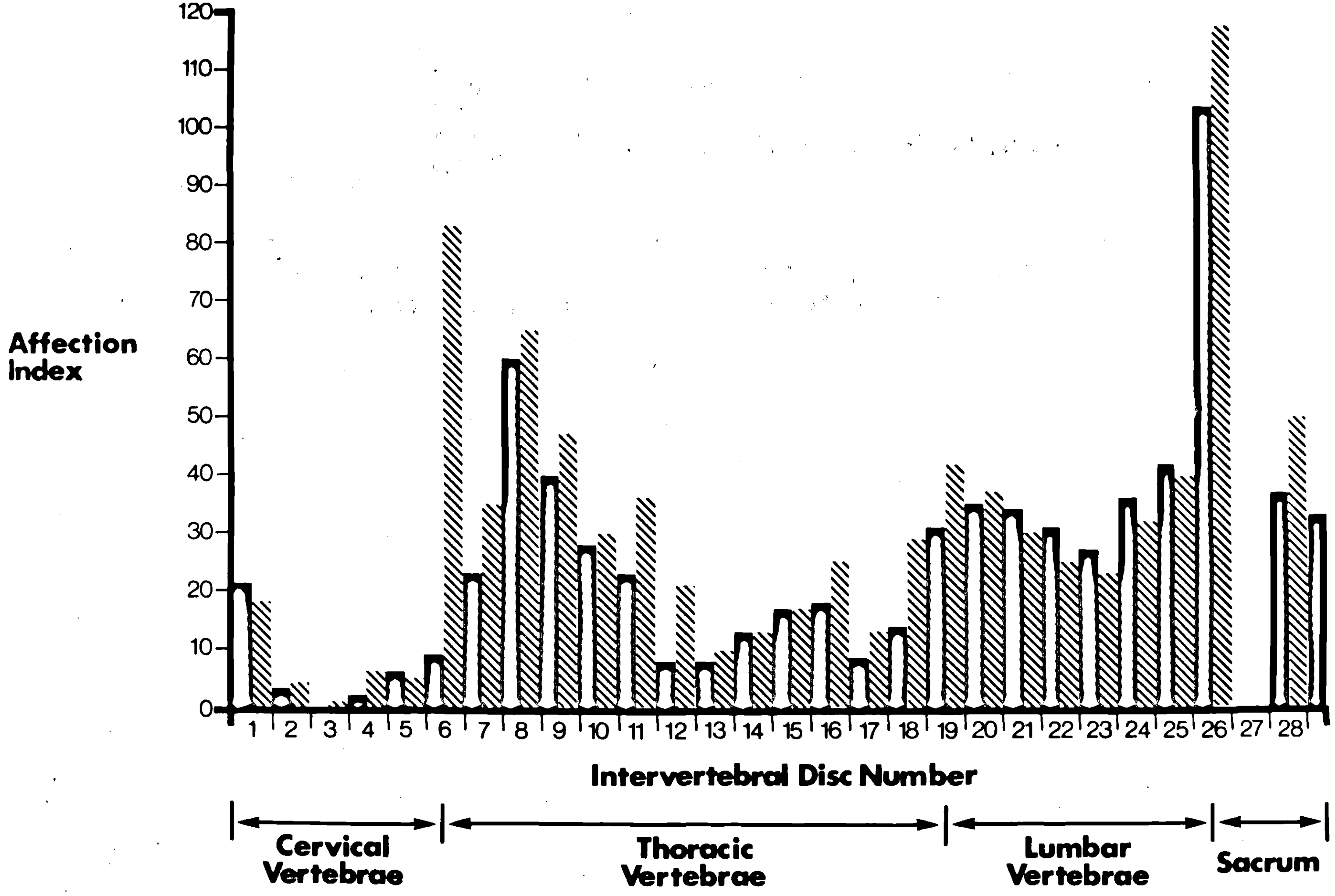

Percentage Occurrence
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Intervertebral Disc Number
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32
34
36
38
40
42
44
46
48
Cervical Vertebrae
Thoracic Vertebrae
Lumbar Vertebrae
Sacrum
Caudal Vertebrae

FIGURE 24 DISTRIBUTION OF SPONDYLOSIS DEFORMANS, SHOWING DEGREE OF AFFECTION (AFFECTION INDEX)

□ ANTERIOR EDGE OF DISC SPACE

▨ POSTERIOR EDGE OF DISC SPACE


Affection Index
120
110
100
90
80
70
60
50
40
30
20
10
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
Intervertebral Disc Number
Cervical Vertebrae
Thoracic Vertebrae
Lumbar Vertebrae
Sacrum

There is a difference in the percentage affection between the anterior and posterior edge of each disc space - throughout nearly the whole length of the vertebral column the posterior edge of the disc space shows a slightly higher percentage affection, 'this difference being markedly exaggerated at disc 6 (cervico-thoracic junction). This trait is least pronounced in the lumbar region, where the normal pattern may even be slightly reversed (Figure 23).

In the cervical and most of the thoracic region only osteophytes of grade I and II are to be found (Figure 25). A few grade III osteophytes are seen in the thoracic region, and most of these are seen in the anterior thoracic region (discs 7-9). In the lumbar and sacral regions a much higher incidence of grade III osteophytes is found, and grade IV osteophytes are only found in the posterior lumbar and sacral regions. Although there is a lower percentage affection in the lumbar and sacral regions than in the thoracic region, larger osteophytes are seen and this gives the highest Affection Index at the lumbo-sacral joint.

6.4.4 Position of Osteophytes on the Vertebral Margin

In the pre-sacral vertebrae there are scarcely any dorsal osteophytes. In the cervical region there are too few osteophytes to ascribe any pattern to their distribution (Figure 26). In the anterior thoracic region, as far posteriorly as disc 9, osteophytes are predominantly lateral in position, mainly affecting the costal articulations. From disc 10 to the thoraco-lumbar junction there is a preponderence of ventral osteophytes. This pattern extends into the anterior lumbar region, although in disc 26 there is a marked increase in lateral osteophytes, these outnumbering ventral osteophytes. In the sacral region, in cases where the vertebrae are not fused, osteophytes are equally distributed between the ventral and two lateral regions.

In the post-sacral vertebrae a different pattern is seen. In the first four caudal vertebrae no dorsal osteophytes are present, and the pattern

FIGURE 25 FREQUENCY DISTRIBUTION OF THE FOUR STAGES OF VERTEBRAL OSTEOPHYTE DEVELOPMENT

▧ STAGE ONE
▭ STAGE TWO
▥ STAGE THREE
▨ STAGE FOUR

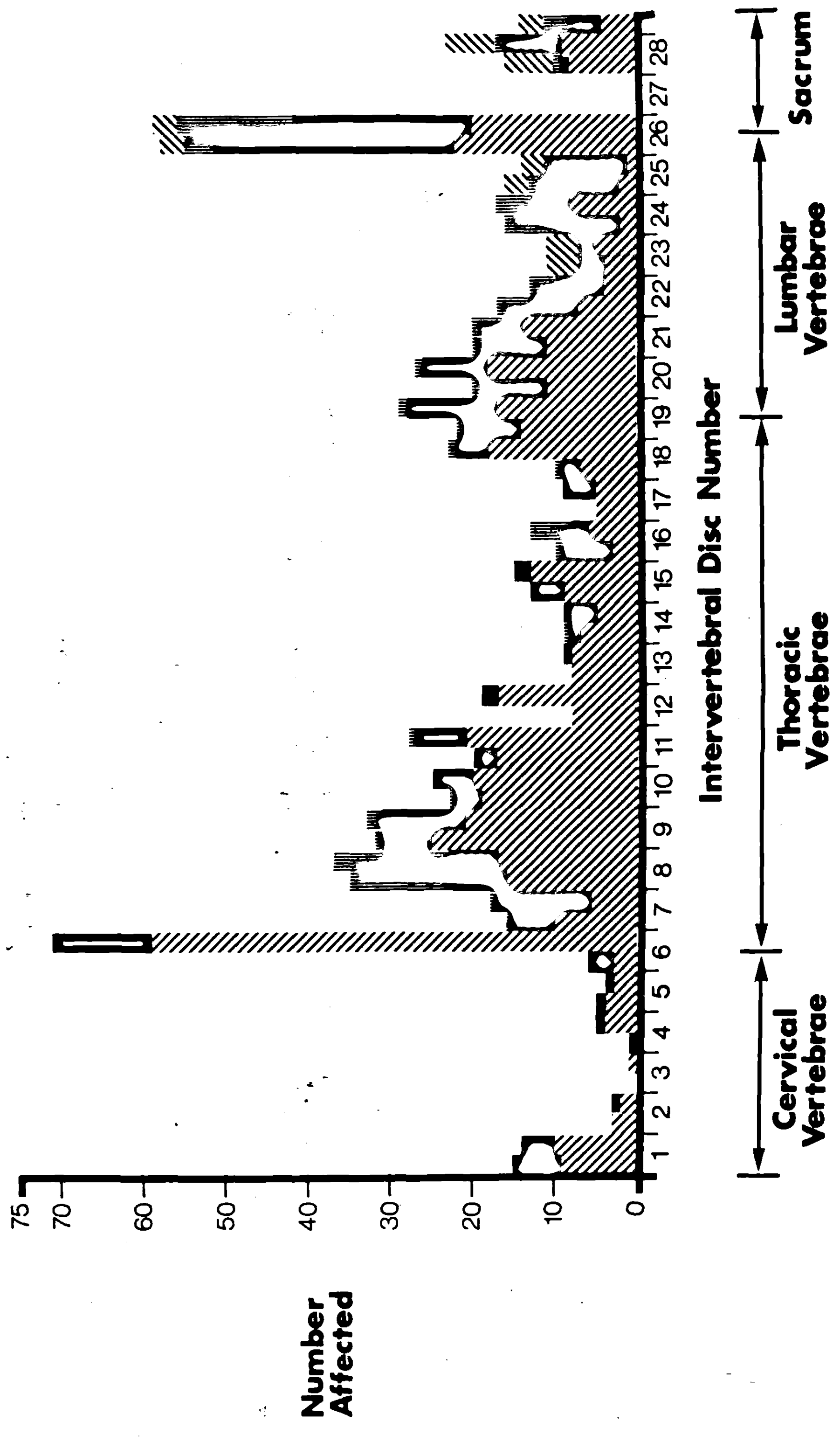
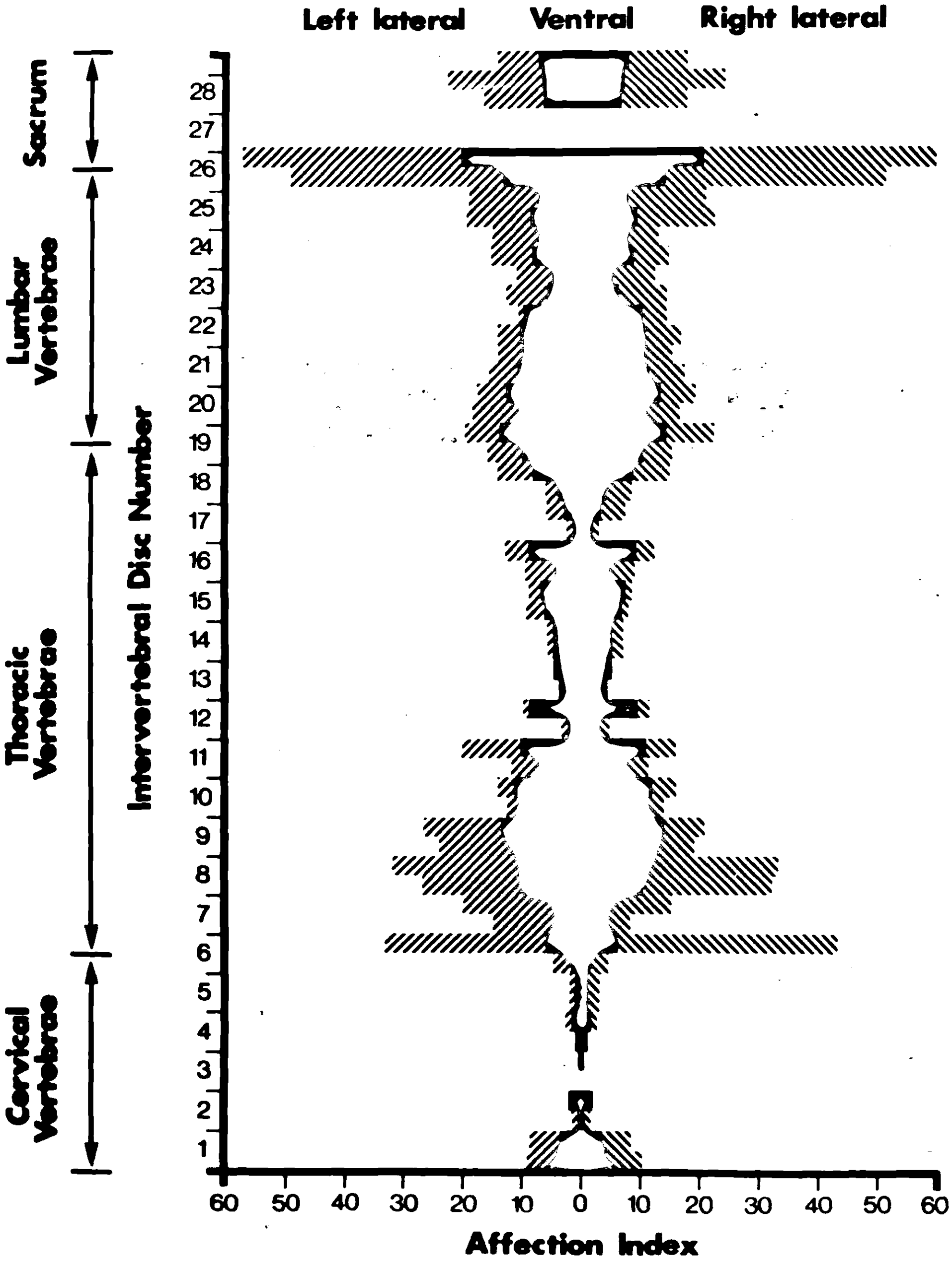

Number Affected
75
70
60
50
40
30
20
10
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
Intervertebral Disc Number
Cervical Vertebrae
Thoracic Vertebrae
Lumbar Vertebrae
Sacrum

FIGURE 26 POSITION OF OSTEOPHYTES ON VERTEBRAL BODY FOR BOTH CRANIAL AND CAUDAL ASPECTS OF INTERVERTEBRAL SPACE


Left lateral
Ventral
Right lateral
Sacrum
Lumbar Vertebrae
Thoracic Vertebrae
Cervical Vertebrae
Intervertebral Disc Number
28
27
26
25
24
23
22
21
20
19
18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
60
50
40
30
20
10
0
10
20
30
40
50
60
Affection Index

of distribution is similar to that observed in the sacral region. In the rest of the caudal vertebrae there are a large number of dorsal osteophytes, and the osteophytes are equally distributed between all four quadrants of the vertebral margin.

6.4.5 Position on the Vertebral Column at which Spondylosis Deformans first appears

To determine the point on the vertebral column at which spondylosis deformans first appears, the 49 animals with an Affection Index of less than 10 were examined. On each animal the intervertebral discs were recorded as either affected or not affected.

Most animals first show signs of affection in the anterior thoracic region (Figure 27), particularly at the cervico-thoracic junction. In the early stages the lumbar region is normally affected to a much lesser extent than the anterior thoracic region, although there is a slight increase in incidence at the lumbo-sacral junction. However, in a few animals only the lumbar region was affected, even in the early stages of affection.

6.4.6 Effects of Age on Spondylosis Deformans

Of the 252 animals used in this study, it was impossible to age one affected female, leaving an aged sample of 251 animals (122 males, 129 females), of which 86 were affected.

There is a marked increase in the incidence of spondylosis deformans with age, so that by the sixth year of life all animals show some signs of the condition (Table 30).

There is also a marked increase with age in the degree of affection (Table 31, Figure 28). In the first two years of life the degree of affection is very low, but there is a marked increase in the third year of life, and

FIGURE 27 INTERVERTEBRAL DISCS AT WHICH SPONDYLOSIS DEFORMANS FIRST APPEARS

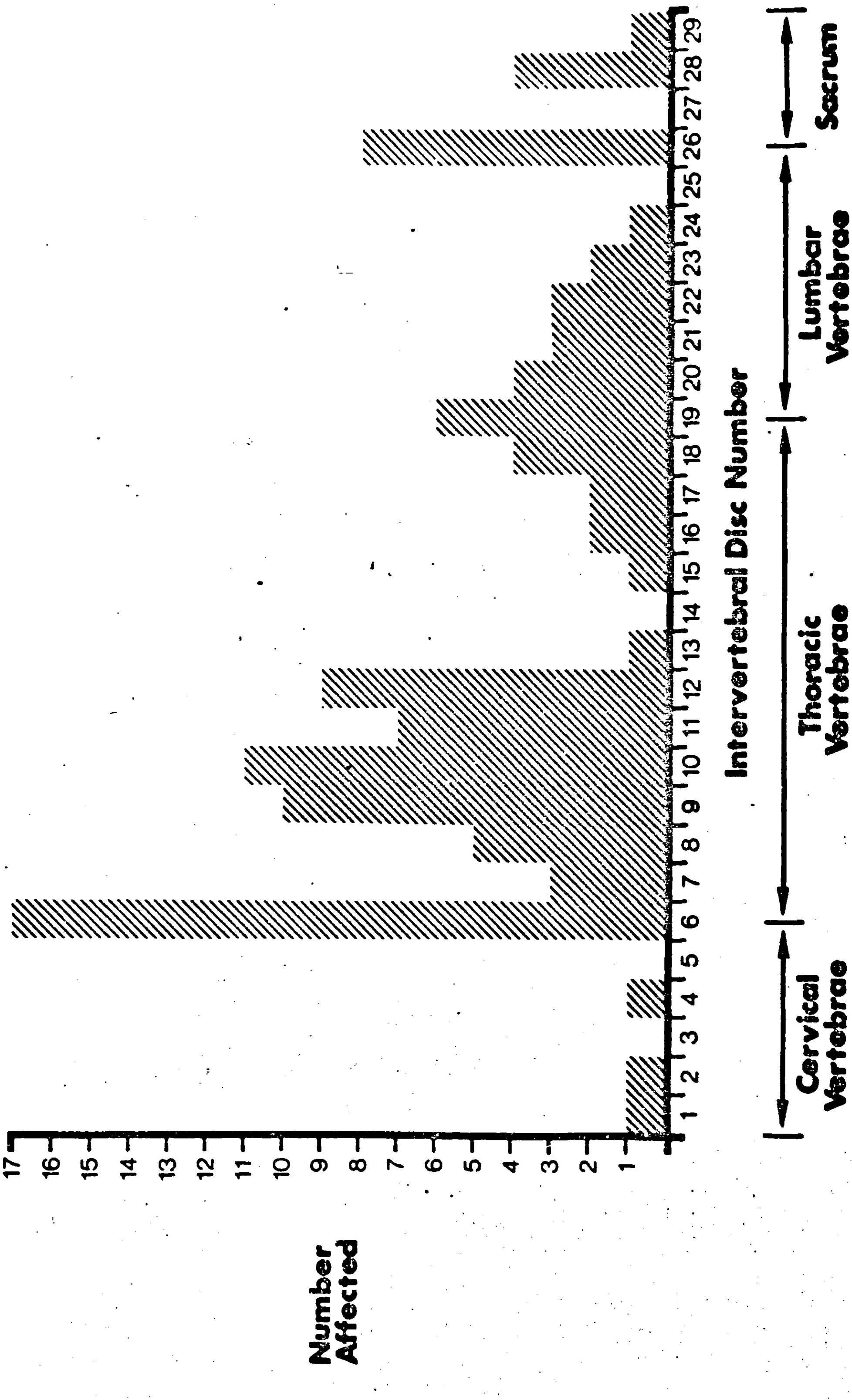

Number Affected
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
Intervertebral Disc Number
Cervical Vertebrae
Thoracic Vertebrae
Lumbar Vertebrae
Sacrum

TABLE 30

INCIDENCE OF SPONDYLOSIS DEFORMANS IN DIFFERENT YEAR CLASSES

Year class	1	2	3	4	5	6	7	8
Number of animals	95	91	31	15	10	7	1	1
Number affected	13	22	20	13	9	7	1	1
Percentage affected	14%	24%	65%	87%	90%	100%	100%	100%

TABLE 31

EFFECT OF AGE ON DEGREE OF AFFECTION BY SPONDYLOSIS DEFORMANS

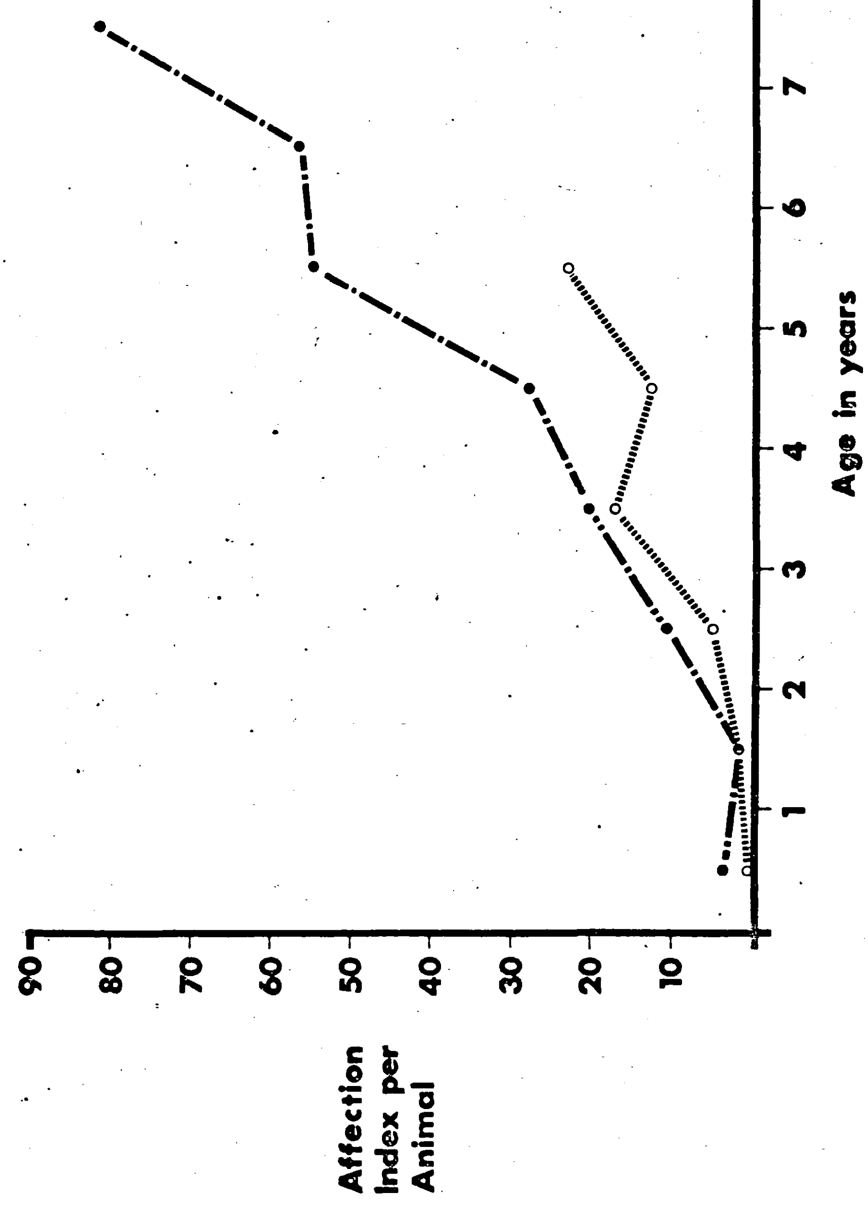
	Males			Females		
Age Class	Number	Total Affection Index	Average Affection Index per animal	Number	Total Affection Index	Average Affection Index per animal
1	52	197	3.79	43	6	0.14
2	36	69	1.92	55	96	1.74
3	15	163	10.87	16	85	5.31
4	6	124	20.67	9	154	17.11
5	5	139	27.80	5	61	12.20
6	6	330	55.00	1	23	23.00
7	1	57	57.00			
8	1	82	82.00			
Total	122	-	-	129	-	-

Comparing males and females up to six years of age, X^2 for 5 degrees of freedom = 5.199. Difference not significant at the level P = 0.1.

FIGURE 28 EFFECT OF AGE ON THE DEGREE OF AFFECTION BY SPONDYLOSIS DEFORMANS

●▬▪▬▪▬● MALES

○┅┅┅┅○ FEMALES


Affection Index per Animal
90
80
70
60
50
40
30
20
10
1
2
3
4
5
6
7
8
Age in years

the degree of affection continues to increase throughout life. The same pattern of increase is seen in both sexes, but for each age class the males show a higher degree of affection (Affection Index) than the females. However this difference is not significant at the level $P = 0.1$.

6.4.7 Effects of Physical Injury on the Development of Spondylosis Deformans

Previous physical injury was defined as any skeletal defect or fracture indicative of a previous accident. Although not clear-cut, this was considered the most reasonable means of detecting the effects of a major trauma on the development of the condition. Physiological traumas, which could equally well affect the development of the condition, could not be recorded and so may well reduce the significance of the results.

Of the 252 animals, 83 (32.94%) showed evidence of previous physical injury, and this was usually the result of a car accident. The usual signs of a previous injury were fractured ribs or long bones, more rarely injuries to the pelvis and/or vertebral column.

In each age class, there was a markedly higher Affection Index per animal in those showing signs of a trauma than those without any such evidence (Table 32, Figure 29). Comparing the first six year classes, the difference between animals showing previous injury and those that don't is not quite significant at the level $P = 0.1$.

6.4.8 Effects of Spondylosis Deformans on the Condition of the Animal

Although it is difficult to examine the effect on an animals' general health of one of several diseases that may be present, it was felt that body weight could be used as a useful guide to health, and so the effect of spondylosis deformans on body weight was examined.

TABLE 32

EFFECT OF PHYSICAL INJURY ON THE DEVELOPMENT OF SPONDYLOSIS DEFORMANS

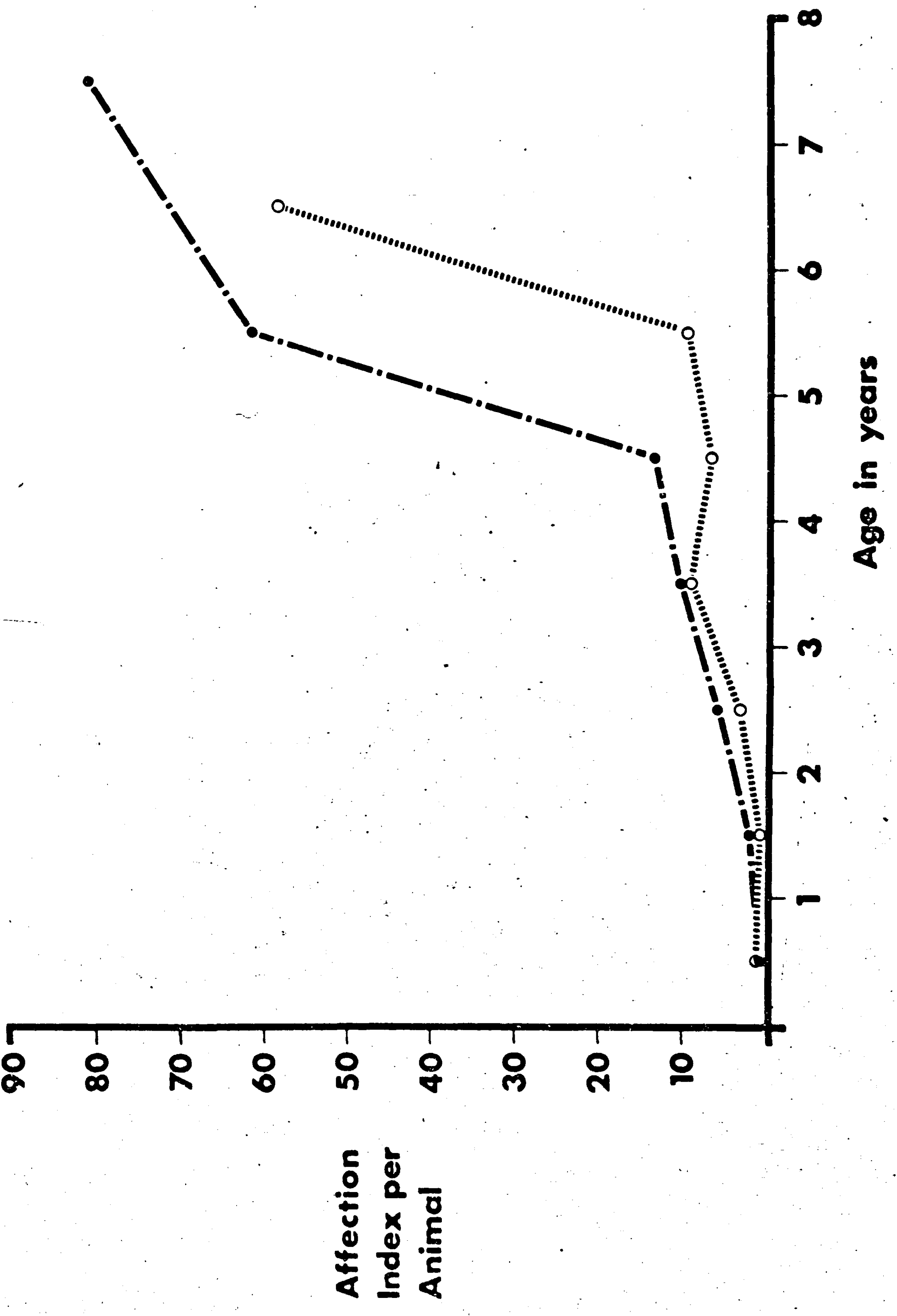
Year Class	Presence/absence injury (+ or -)	Number of animals	Total affection index	Average affection index per animal
1	-	67	153	2.28
	+	28	50	1.79
2	-	67	87	1.30
	+	24	78	3.25
3	-	20	125	6.25
	+	11	123	11.18
4	-	8	144	18.0
	+	7	134	19.14
5	-	5	67	13.4
	+	5	133	26.6
6	-	2	38	19.0
	+	5	315	63.0
7	-	1	57	57.0
	+	0	-	-
8	-	0	-	-
	+	1	82	82.0

Comparing the first six year classes, X^2 for 5 degrees of freedom = 8.740. Difference not significant at the level $P = 0.1$.

FIGURE 29 EFFECT OF PHYSICAL INJURY ON THE DEGREE OF AFFECTION BY SPONDYLOSIS DEFORMANS

○┅┅┅┅┅┅○ NO PREVIOUS INJURY

●▪▪━━▪━━● PREVIOUS INJURY


Affection Index per Animal
90
80
70
60
50
40
30
20
10
1
2
3
4
5
6
7
8
Age in years

The eviscerated body weight was recorded for 35 of 42 affected females, and 38 of 45 affected males. The other animals were too badly injured during collection to make weighing worthwhile.

Although the sample size for the higher levels of affection is small, general trends are apparent. Figure 30 and Table 33 show that in both sexes the body weight increases until an Affection Index of 41-50 is reached, this being due to the increasing age of the animals. With greater levels of affection there is a marked decrease in body weight, which in the males amounts to 20 - 25%. The only exception to this were the two males in the group with an Affection Index of 31 to 40, and both these animals were in poor condition due to other injuries.

6.4.9 Variations in the Vertebral Column

Many variations in the vertebral column were documented. Individual variations in the shape of vertebrae were common, particularly the development of long transverse processes to the first lumbar vertebra, variations in the degree of development of the transverse process and transverse foramen of cervical six, degree of development of the transverse process of cervical seven, fusion of thoracic ten and eleven (the anticlinal vertebra) by their neural spines, and in the fusion of some of the sacral elements to the pelvis.

There were also variations from the normal number of vertebrae ($C_7\ T_{13}\ L_7\ S_3\ Cy_{17-21}$). The number of caudal vertebrae is normally variable, and the number of cervical vertebrae was constant in the sample examined. However the number of thoracic vertebrae was often reduced to twelve or increased to fourteen, usually associated with an increase in the number of lumbar vertebrae to eight or a partial sacralisation of the last lumbar vertebra respectively. Sometimes the change was complete, sometimes a vertebra intermediate in morphology was found. All such variations were ignored in recording the osteophytes present, since they had no effect on the development of the condition.

TABLE 33

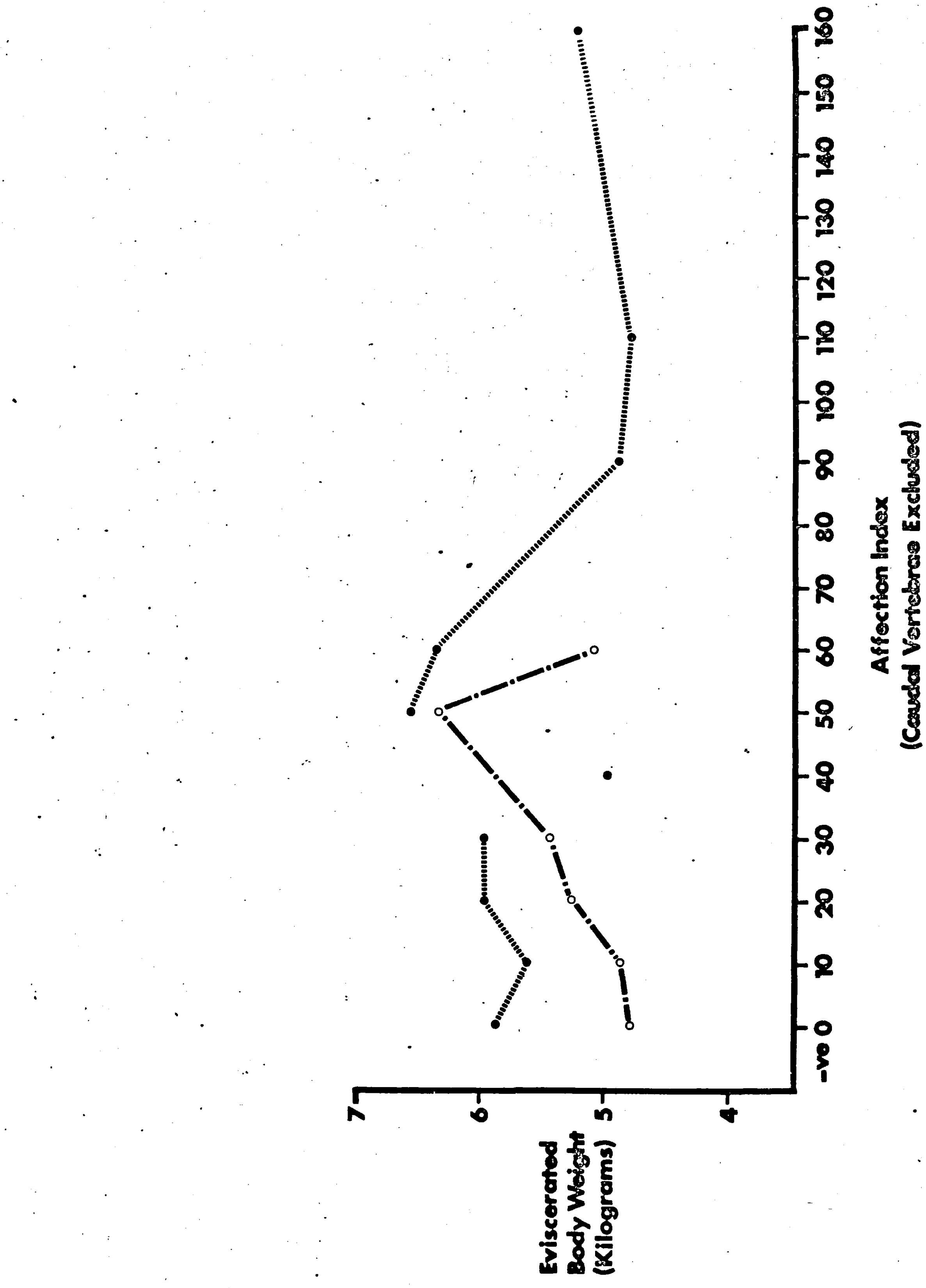
EFFECT OF SPONDYLOSIS DEFORMANS ON CONDITION (BODY WEIGHT) OF AFFECTED ANIMALS

Affection Index	Males		Females	
	Number	Average weight in kilograms	Number	Average weight in kilograms
0	68	5.87	79	4.80
1-10	13	5.67	25	4.87
11-20	10	5.97	5	5.27
21-30	4	5.96	3	5.44
31-40	2	4.99		
41-50	4	6.57	1	6.35
51-60	2	6.24	1	5.10
61-70				
71-80				
81-90	1	4.90		
91-100				
101-110	1	4.80		
111-120				
121-130				
131-140				
141-150				
151-160	1	5.24		

FIGURE 30 EFFECT OF SPONDYLOSIS DEFORMANS ON THE CONDITION (BODY WEIGHT) OF THE ANIMAL

● ┅┅┅┅┅ ● MALES

○ ▪▪━ ▪ ━▪▪ ○ FEMALES


Eviscerated Body Weight (Kilograms)
7
6
5
4
-ve 0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
Affection Index (Caudal Vertebrae Excluded)

Variations in the sacral vertebrae were important in the course of development of spondylosis deformans, and these variations are presented here (Table 34). The failure of any sacral element to fuse completely caused marked development of osteophytes between the unfused elements, as shown on Figure 25, where many osteophytes are present between S_2 and S_3. In all, 46/252 (18.25%) of the sacra exhibited some anomaly.

6.5 DISCUSSION

6.5.1 Number of Animals Affected

For a random sample, taken from a population with a very low life expectancy, an overall affection level of 34.5% is very high. There are no comparable data for any other wild animal population, but such an affection level would be considered high even in a population of domestic animals.

Beadman, Smith & King (1964) found 102/150 cats were affected, giving a frequency occurrence of 68%. Similarly Read & Smith (1968) found 67.6% of 176 English cats and 34% of 100 Swedish cats were affected.

There have been a number of surveys into the incidence of spondylosis deformans in domestic dogs. Hansen (1951, 1952) described a "chondrodystrophoid breed group" for dogs particularly exposed to disc degeneration. Hansen (1952) further found that degeneration of the intervertebral discs in chondrodystrophoid breeds usually led to what he described as type I protrusions without associated spondylosis deformans. But disc degeneration in dogs of non-chondrodystrophoid breeds, as well as in discs in old dogs of chondrodystrophoid breeds, resulted in type II disc protrusions and/or spondylosis deformans. Thus Hansen found that of 211 chondrodystrophoid dogs 12 (5.7%) were affected with spondylosis deformans, while 37/350 (10.6%) of non-chondrodystrophoid breeds were

TABLE 34

VARIATIONS IN THE STRUCTURE OF THE SACRUM OF THE RED FOX

Type of Variation	Number of Occurrences
Only first two elements of sacrum fused	26
Third element of sacrum only fused by lateral crests	8
Fourth sacral element present but completely free	1
Fourth sacral element only fused by lateral crests	2
Fourth sacral element completely fused	2
Last lumbar element sacralised but separate; sacrum only two elements	1
Last lumbar element part-fused to sacrum; sacrum only two elements	2
Last lumbar element part-fused to sacrum; sacrum three elements	1
Additional eighth lumbar element part-fused to sacrum; sacrum three elements	2
Last lumbar element completely fused to sacrum; sacrum only two elements	1

affected. Morgan (1967) found that 71/116 animals (61%) were affected. Following Hansen's definition of chondrodystrophoid breeds, Morgan found that 22/29 (76%) of chondrodystrophoid animals were affected, while in non-chondrodystrophoid breeds only 49/87 (56%) were affected. However this difference was not statistically significant. Morgan also noted that his low incidence in Dachsunds, as compared to Boxers and German shepherd dogs, was in agreement with Hansen's finding that chondrodystrophoid breeds were less prone to spondylosis than were non-chondrodystrophoid breeds. Morgan, Ljunggren & Read (1967) compared samples of dogs from England, Sweden and the USA. They found that the frequency of affection for the three countries was as follows: England 110/144 (62.8%); Sweden 36/223 (16.2%); USA 48/206 (23.3%). The higher incidence from England was attributed to a more efficient radiographic technique, whereby it was less likely that small osteophytes were missed. Bellars & Godsal (1969) noted that 9/11 British Antarctic Survey Sledge dogs were affected, although they also noted that the changes were less severe than those seen in large dogs of similar ages in the United Kingdom.

Some breeds of dogs are thought to be more prone to spondylosis deformans - Morgan (1967) noted a low incidence in Dachsunds, whereas Glenney (1956) noted the highest incidence in Dachsunds, and Archibald & Cawley (1966) also noted a high incidence in this breed, as well as in large dogs such as Great Danes and Boxers. Hansen (1952) also noted a high incidence in Boxers and Fox terriers, and Morgan (1967) noted a high incidence in Boxers and German shepherds.

The important point to stress is that most of these studies on domestic animals were based on cadavers collected from veterinary surgeons, and the average age of the material was high. The average age of the foxes used in this study was only 1 yr. 9 mths., and none of the studies mentioned above recorded a 34.5% occurrence of spondylosis deformans in such a young population.

This present study has shown a slightly higher incidence in males (36.9%) than in females (32.3%). Morgan (1967) also found a slightly higher incidence in males (64%) than females (59%) but in neither case was the difference statistically significant. Read & Smith (1968) in samples of English cats, Swedish cats and English dogs found in each group a slightly higher percentage affection in males than females. However Morgan, Ljunggren & Read (1967) found that in all three of their samples of dogs, females were more affected than males. Similar differences of opinion are expressed by workers who studied the human spine. Nathan (1962) found a higher incidence in males than females in both whites and negroes. Roche (1957) found a higher incidence in females than in males, but with increasing age the incidence in males equalled or exceeded that found in females. Schmorl & Junghanns (1959) found that the sex difference in 4,253 human thoracolumbar spines was less significant than generally assumed, but males always had a higher level of affection than females.

Wells (1964) noted that in Saxon skeletons women were equally affected with men, with a total frequency of nearly 100%, but in Pecos Pueblo skeletons less than one person in seven exhibited the condition, and here males were affected three times as often as females. Wells took this to indicate a sexual division of occupations, and also suggested that the second situation may indicate a better relative status for the women.

In some species there is a marked sex difference in the incidence of spondylosis deformans. Anon.(1956/7) noted that spondylosis deformans was extremely common in bulls, while it was rare in cows, and Jubb & Kennedy (1963) described ankylosing spondylosis as an occupational hazard of bulls kept in artificial insemination studs. However Frank (1939) described two affected cows and one bull, and made no reference to an increased occurrence in bulls. Jubb & Kennedy (1963) also described this condition as not uncommon in adult sows but not boars, the reverse of the situation seen in bovines.

6.5.2 Degree of Affection

There are no comparable data showing the degree of affection throughout a population, and so no comparisons can be drawn with the data presented here.

Why the male foxes show a higher degree of affection than females is uncertain; presumably some ecological or physiological difference between the sexes is important here but it is impossible to determine exactly which factor(s). Weight may be important in this respect (see 6.5.8) and dog foxes are heavier than vixens (Section 3).

6.5.3 Distribution of Osteophytes along the Vertebral Column

The general pattern of distribution of osteophytes in the fox is for the highest incidence to occur at the cervico-thoracic, thoraco-lumbar and lumbo-sacral junctions, with another aggregation in the anterior thoracic region. There is a minor increase at the anticlinal (11th. thoracic) vertebra, and there is generally a dearth of osteophytes in the cervical region.

Fox (1939) noted that in the Carnivora as a whole arthritis is more prominent posterior to the cervical vertebrae. It continues to be prominent along the thoracic spine, becomes quite marked in the upper lumbar region, and almost disappears towards the sacrum. He noted that the points of greatest affection were the sixth and twelfth thoracic and first to fourth lumbar vertebrae. This pattern seen in the order as a whole is different from that seen in the present study, but it must be remembered that Fox included the Ursidae, which show a nearly uniform pattern of osteophytes from the lower neck to the sacrum, and the Hyaenidae, which also show osteophytes all along the spine, with the greatest prominence in the low thoracic and lumbar sections. It must also be remembered that Fox noted that wild Canidae do not exhibit any form of arthritis, so no representatives of the family were included in his total sample.

The pattern of distribution of osteophytes in the fox shows similarities to that seen in both the cat and the Domestic dog. Hansen (1952) noted that in dogs changes are localized, especially in the thoracic and lumbar parts of the vertebral column, with the greatest incidence at disc 26 (lumbo-sacral junction), and with a lower incidence at discs 10/11 (thoracic 4-6) and possibly disc 15 (thoracic 9-10). Glenney (1956) noted that in dogs osteophytes are seen predominantly in the last two or three thoracic and any of the lumbar vertebrae. Morgan (1967) gave a detailed account of the distribution of lesions in Swedish dogs. Although the basic pattern of distribution is similar to that seen in the fox, a number of important differences occur. The high incidence at the cervico-thoracic junction, present in the fox material, is not seen in dogs. Similarly the gradual increase in the number of osteophytes seen in the thoracic region of the dog, reaching a maximum at disc 15, is not seen in the fox, although there is a very slight increase around the anticlinal vertebra. Both fox and dog samples show a slight increase around disc 20, and both show a major occurrence at disc 26. Morgan, Ljunggren & Read (1967) also described the distribution of osteophytes along the dog vertebral column. The general pattern was very similar to that described by Morgan (1967) but between the three samples they noted some differences - two samples showed a small peak at thoracic 5-6, whilst the third sample had a large peak at thoracic 9-10 not matched by the other samples. In all three of these samples a paucity of lesions was noted in the cervico-thoracic area, whereas in the fox the highest percentage occurrence of osteophytes was seen here (although the Affection Index was low since all osteophytes were small).

Beadman, Smith & King (1964) described the distribution of osteophytes along the cat vertebral column. They described a uniform, and relatively high, number of osteophytes at each disc in the cervical region, with a slight increase at disc 1 - this is also seen in the fox. They also noted a slight increase at the cervico-thoracic junction, whereas in the fox there was a marked occurrence at this point. The cat was found to show a higher number of osteophytes in the thoracic than in the lumbar regions, and although a similar general pattern was seen in the fox, it was not nearly so pronounced. There was no increase at the lumbo-sacral junction in the cat. Read & Smith (1968) compared two cat samples, and found a similar pattern of distribution to that found by Beadman, Smith & King (1964). Read & Smith also noted that there was no correlation between the distribution of osteophytes in the dog and cat.

In man the distribution is somewhat different. Beadle (1931) recorded that most osteophytes are seen from the 4th or 5th dorsal vertebra downwards, including the whole lumbar spine, whereas Nathan (1962) showed a high cervical, especially late cervical, low early thoracic, and high late-thoracic and lumbar incidence. This is almost exactly the reverse of the situation seen in the cat.

In the fox no osteophytes were noted on the atlas nor the odontoid process of the axis. This lack of osteophytes was also noted by Beadman, Smith & King (1964) in the cat and Morgan (1967) in the dog. However in man the atlanto-epistrophic joint may be affected, and Stewart (1958) noted that whites have more "lipping" in the cervical region, especially in the atlanto-epistrophic joint, than do Eskimos and Pueblo Indians, and Bailey & Casamajor (1911) noted that exostoses from the odonto-atloid joint cause compression of the medulla.

Morgan (1967) compared several distribution patterns of osteophytes, and noted that in each species examined (dog, cat, man and bull) there was a distinct characteristic distribution pattern, and that this probably reflects a difference in the bio-mechanics of the vertebral columns. This could mean that factors such as posture, type of physical activity, and range of mobility of different segments of the vertebral column are of importance for the occurrence of disc changes, and that these disc changes may then cause the occurrence of osteophytes. Read & Smith (1968) suggested that different methods of movement might influence the pattern of distribution of the osteophytes. However, Morgan, Ljunggren & Read (1967) tried to establish possible correlations between areas of higher incidence and factors such as normal or abnormal spinal motion, and areas of ligamentous attachment, but they found that none of these factors alone were adequate in providing a satisfactory explanation of the variable frequency of lesions.

In bulls, where the bulk of the osteophytes are found in the lower thoracic and lumbar spine, Anon.(1956/7) attributes the activating causes that induce osteophyte formation to the stresses to the joints of the spine during mounting and service reflexes. Another case where the local abundance of osteophytes is easily explained is in the human spine, where Shore (1935) and later Nathan (1962) found that osteophytes tended to appear where the pressure is greatest - the peaks of regional distribution were related to the normal curvatures of the vertebral column and the diminution zones are found at the balanced vertebrae through which the weight of the trunk falls vertically; these latter vertebrae mark the points of relative stasis in relation to posture and the ordinary movements of the erect-standing man.

There is some variation as to which side of the disc showed the greater affection level. In the fox nearly every disc showed a greater percentage affection on the posterior edge of the disc. Beadman, Smith & King (1964) showed that in the cat intervertebral discs from cervical 6-7 to the end of the thoracic vertebrae it was the caudal part of the disc which was uniformly more commonly affected than the cranial, as seen in the fox, whereas in the remainder of the discs the cranial end was more frequently affected. Read & Smith (1968) noted the same distribution pattern in their samples of Swedish and English cats. These last two authors also studied a sample of English dogs, and found the reverse pattern to that seen in the cat - in the dog most thoracic intervertebral discs are more commonly affected on the cranial edge, whereas most of the lumbar spaces are more commonly affected on the caudal edge, the exception being the lumbo-sacral space where the lumbar edge was more often affected than the sacral edge. This reversal of the distribution pattern at the lumbo-sacral junction was not seen in the fox.

Although Nathan (1962) first used the system of recording the size of the osteophytes he did not show the distribution along the spine of each stage of development of the osteophytes. Morgan (1967) presented these data for the dog, although as previously noted he introduced an earlier stage, so that stages 2-5 of Morgan are equivalent to stages 1-4 used by Nathan and in the present study. Overall, Morgan found a much lower occurrence of the earlier stages of development of osteophytes than was seen in the fox. Thus Morgan noted that in the cervical region most of the osteophytes were small, with only two cases of fusion. However in the fox no osteophytes larger than grade 2 were recorded from this region. Morgan found that the majority of spurs in the thoracic region were stages 2 and 3, which is also true in the fox, but again Morgan found more of the larger osteophytes, including cases of fusion, which were not seen in the thoracic region of foxes. In the lumbar region of the dog Morgan stated that most osteophytes were of stages 3 and 4, and that the number of stage 5 spurs was greater than in other areas of the vertebral column. In the pre-caudal region of the fox the only fused osteophytes were found in the posterior lumber region (disc 23 backwards), and the sacrum when the sacral elements were not fused. Again a higher percentage of large osteophytes was seen in the dog. (The highest number of fused osteophytes were seen in the caudal vertebrae of the fox, but as explained this data could not be analysed completely.)

6.5.4 Position of Osteophytes on the Vertebral Margin

The position of the osteophytes on the vertebral margin was very similar to that described by Morgan (1967) for the dog. In the dog Morgan found that the majority of the spurs in the cervical region were located on the ventral midline, whereas in the fox there were so few osteophytes in this region that it was not possible to note any clear pattern. Morgan noted that these spurs represented a continuation of the prominent ventral ridge as found especially on C_{2-4}. He further found that from disc spaces 7-17 the pattern had changed, with approximately 2/3 of the spurs equally divided to the right and left of the midline. In the fox these laterally placed spurs were only prominent over a much shorter distance - the posterior face of disc 6 to disc 9, and thereafter the majority of the spurs were ventral, with the exception of discs 25 and 26, where the spurs were equally divided between all three faces. In the dog Morgan found that the majority of osteophytes occurred in the midline only from disc 18 to 23, whereas from disc 24 to the lumbo-sacral junction the majority of the spurs were on the lateral aspects of the vertebral margin. Both studies agreed on the paucity of dorsal osteophytes.

Although both the dog and fox studies have found the osteophytes to occur evenly on both sides of the vertebral column, the same situation is not seen in man. Beadle (1931) noted that in the dorsal spine osteophytes were predominantly on the right side, lumbar osteophytes predominantly to the left. Tobin & Stewart (1953) accounted for this unequal distribution by claiming that thoracic osteophytes occurred mainly on the left side in right-handed persons and vice versa. Schorr, Fränkel & Adler (1957) showed that right unilateral thoracic spondylosis was not related to right-handedness. Culver & Pirson (1956), Shapiro & Batt (1960) and Nathan (1962) demonstrated that the distribution of osteophytes was related to the position of the aorta - Shapiro & Batt (1960) suggested that normal aortic pulsations produce physiologic resorption of bone. Nathan (1962) also commentated that where the aorta occurs on the mid-line osteophytes occur symmetrically on both sides of the vertebrae. Since the aorta in canids occurs nearly mid-ventrally (Miller 1952) the symmetrical occurrence of the osteophytes in the thorax is readily explained.

The absence of dorsal osteophytes is common to all studies. Collins (1949) pointed out that in man osteophytes rarely form on the posterior surface because collapsed discs are always compressed anteriorly, and the bony spurs grow to enclose the extruded disc. Morgan (1967) also noted the rarity of dorsal osteophytes, and in none of the cases he examined had the osteophytes encroached on the spinal canal to an appreciable extent. However, in adult sows Jubb & Kennedy (1963) reported that extensive new bone formation may occur in the neural arches, which fuses the articular processes and encroaches on the spinal canal, giving it an irregular or triangular shape. In the fox, however, the presence of the neural canal seems to directly inhibit the development of the dorsal osteophytes.

In the caudal vertebrae of the fox osteophytes occur equally on all four quarters of the vertebral margin, dorsal osteophytes being pronounced in the absence of the neural canal. There is no comparable data for the dog and the cat, Morgan (1967) did report that spurs were frequently located around the coccygeal discs although their location and number were not recorded.

Morgan (1967) discussed the role of the ventral longitudinal ligament in osteophyte formation, and showed that it was influential only in determining the characteristic shape of the vertebral osteophytes - it did not initiate their formation, and so does not affect the position of the osteophytes on the vertebral margin.

6.5.5 Position on the Vertebral Column at which Spondylosis Deformans First Appears

It was shown that when spondylosis first appears the thoracic region is both more often affected, and also shows a higher Affection Index, than the lumbar region: only when the animal is badly affectly does the lumbar region show an Affection Index similar to that seen in the thoracic region.

This trait of the thoracic region to be affected earlier has been noted in the human spine by several workers. Schmorl & Junghanns (1959) noted that spondylosis was limited to the thoracic spine more frequently in the young than the old: severe spondylosis in the lumbar spine with a lesser degree in the thoracic spine, and also severe spondylosis in both lumbar and thoracic regions both show a greater increase with advancing age. Nathan (1962) noted that anterior osteophytes develop earlier in the thoracic and lumbar regions than in the cervical and sacral regions, as was also found to occur in the fox. Similarly, in the human spine, Bick (1964) noted that vertebral osteophytes usually appear first in the dorsal spine and then with more or less equal timing and frequency in the mid-cervical and lower lumbar spines.

Anon. (1956/7) reported that in bulls the disease commonly develops in the 6th-7th thoracic articulation and then moves progressively backwards to involve a series of articulations.

In contrast, Morgan, Ljunggren & Read (1967) found the reverse in the dog. They showed that the average size of the osteophytes was similar throughout the vertebral column and suggested that this indicated no difference in "age" of the osteophytes as related to their location along the vertebral column.

Shore (1935) noted that in the human spine osteophytes are almost never found on a single unit of the vertebral column - their incidence is spread over a group or over more than one group of adjacent vertebrae. These observations would seem to be at variance with those authors who found that spondylosis first appears in a particular (limited) region and then spreads along the vertebral column. Certainly in the present study it was found that during the early stages of affection only one or two vertebrae exhibited osteophytes.

6.5.6 Effects of Age on Spondylosis Deformans

That the development of spondylosis is associated with ageing has been known for a long time, and Glenney (1956) described spondylosis as a geriatric problem. Since spondylosis is so invariably associated with ageing, the appearance and development of vertebral osteophytes must be regarded as normal, and this condition can only be described as pathological if there is an acceleration of the normal degenerative processes due to dietary deficiencies, trauma, etc., or when pain and locomotor debility ensues.

The most interesting feature about spondylosis in the fox population examined is its rapid development - 65% of the population are affected in their third year of life, 90% in their fifth year, and all animals from their sixth year onwards are affected. This contrasts markedly with the observations of Morgan, Ljunggren & Read (1967), who noted that in their three dog samples the earliest case of spondylosis occurred during the second year of life in two groups and in the third year in the other group.

This rate of development in the fox is significantly faster than that seen in bulls. Anon. (1956/7) recorded that "ankylosing spondylosis commences at or about the age of five years" and it is "almost exceptional for it to be absent in bulls over the age of 6½ years". The fox data show a considerably greater rate of development than Morgan (1967) recorded for domestic dogs - he found that 50% were affected by three to six years of age, 75% by nine years, and in older dogs the figure approached 100%. Morgan also found that most of the formation of osteophytes in the dog took place in middle age. A similar conclusion was reached by Glenney (1956), who reported that in the dog spondylosis occurred at middle age and after, although it could occur in animals eighteen to twenty-four months old.

The rate of development of spondylosis has been well documented in man. Stewart (1958) noted that in each of the cervical, thoracic and lumbar regions of the spine lipping develops slowly through the age of 30, intensifies in the fourth decade, especially in the lumbar region, and becomes quite pronounced after 50. Whichever species is studied, a small number of individuals never seem to develop spondylosis, and Stewart noted that even in the eighth decade a small proportion of individuals do not show any signs of vertebral lipping. However Nathan (1962) gave a slightly different time scale - he stated that spinal columns first showed osteophytes in the twenties, and by the forties all specimens examined showed osteophytes. Nathan also showed an increase in the size of the osteophytes with age - by the fifties nearly all skeletons showed at least some second degree osteophytes, and by the eighties nearly all vertebral columns showed third or fourth degree osteophytes. Bick (1964) showed a time-scale much more similar to that of Stewart (1958), claiming that spondylosis was found in many persons past the age of 35, and was all but universal past the age of 65 or 70.

In view of this very rapid development in the fox, where animals only a few months old show extensive osteophyte formation, it would appear that in this animal spondylosis is not just a normal degenerative process but also a pathological condition. The reasons for this condition being regarded as at least partly pathological in the fox will be discussed later.

6.5.7 Effects of Physical Injury on the Development of Spondylosis Deformans

Schmorl, in his extensive works on the human spine, first showed that degenerative changes in the intervertebral discs were the predisposing causes of spondylosis deformans (and other vertebral abnormalities), although disc degeneration was not invariably followed by exostoses. However several factors affect the course of affection. Glenney (1956) suggested that vitamin A deficiency in dogs accentuated the development of spondylosis. Feldman & Colson (1933) in pigs and Frank (1939) in cattle associated spondylosis with bacteria of the Brucella group, and Nathan (1916) induced spondylosis in dogs by injecting streptococci into the femoral vein. Nathan (1962) notes staphylococcal or other bacterial infections as sometimes being important in the development of spondylosis.

Trauma has also been reported by several workers as being important in the development of spondylosis. Bick (1964) reported that vertebral osteophytes may develop at any age following a trauma. Trauma may take any one of several forms - in the present study previous physical injury was examined as a predisposing factor in the development of spondylosis, this being recognised by the presence of fractured bones. Although not included in the present examination, other bone disorders could also be important in this respect - Nathan (1962) includes infectious osteitis due to tuberculosis, rickets, osteoporosis, and others as being traumatic conditions that may affect the development of spondylosis, and Payne (1959) noted that trauma, either massive or insidious wear and tear, was important in initiating intervertebral disc disturbance.

Since traumas other than bone fractures can affect spondylosis, these must affect the results of a direct comparison between those animals with signs of a previous fracture, and those without. Yet despite these masking effects, in each age class animals with signs of a previous bone fracture showed a higher incidence of spondylosis than those without. However, animals without signs of an early injury can also show well-developed spondylosis, so trauma only accentuates the condition and is not the sole reason for it. That trauma speeds the development of spondylosis was reported by Schmorl & Junghanns (1959), who quote the findings of Heinrich & Städter that it takes at least eighteen months for the formation of a noticeable spur in man, but following spinal injury the beginnings of marginal overgrowths have been observed within four to eight weeks.

Garvin (1927) thought it improbable "that a single accident or injury is responsible for the development of hypertrophic arthritis of the spine". In contrast, however, Chapman & Chapman (1969a) recorded that twelve out of twenty-four skeletons of road-killed Dama dama exhibited degenerative lesions of various sorts, including spondylosis, which were attributed to earlier accidents, usually road accidents or gun-shot wounds.

The effects of trauma in accentuating the development of spondylosis deformans is obvious, but this is only one of many complex factors which interact to affect the development of the condition. This view is in support of Morgan, Ljunggren & Read (1967), who tried to establish a correlation between areas of higher incidence and factors which included trauma, but found that none of these factors alone seemed adequate in providing a satisfactory explanation of the variable frequency of lesions. In contrast, however, Wells (1964) noted different peaks of distribution along the spine depending upon the main focus of any stresses - he noted that in pre-Roman wild horses spondylosis affects the dorsal region of the spine, whereas in modern riding and working horses it is the lumbar region which is attacked. Wells noted a similar dispartiy in human spines - in ancient Egyptians spondylosis was present both severely and relatively often in the thoracic segments, whereas in modern European populations the lower lumbar region is the site of election, and in this latter group this is the site of a perpendicular thrust of 10 or 12 stone in weight. The average ancient Egyptian was slimmer and lighter than the average German, Swede or American today, and it is suggested that this may account for the comparatively low incidence of fifth lumbar damage in ancient Egyptians. Wells suggested that another form of trauma that may cause this difference is that Egyptians did not compress their lumbar discs by slouching in easy chairs or by slumping over office desks.

In the present study, the high incidence of skeletal fractures (33%) is of interest in itself, since it is higher than many previous surveys have found. Chapman & Chapman (1969a) found that 50% of 24 Fallow deer (Dama dama) from Epping Forest had been involved in previous accidents; Taylor (1971) found that 15% of 308 viverrids had diseased or fractured bones as a result of climbing or car accidents. Birkhead (1973) found that 15 of 186 (8%) of corvid skulls showed visible deformities.

6.5.8 Effects of Spondylosis Deformans on the Condition of the Animal

The effects of trauma on the pathogenesis of spondylosis has been discussed, using old fractures as an indicator of an earlier physical trauma. Physiological trauma is also important in this respect, particularly adrenal dysfunction and overweight. Schorr, Fränkel & Adler (1957) noted that thoracic spondylosis was found mainly in overweight males and females of the pyknic type. Similarly in man Nathan (1962) suggested that the higher incidence of spondylosis in males may be attributable to the greater pressure exerted in the vertebral columns of men because of their greater body weight. The same is seen in animals - Fox (1939) reported that varieties with arthritis are macrosomic i.e. coarser, heavier animals. Morgan (1967) examined the incidence of spondylosis in dogs with relation to body weight, and found the condition to be present in 18/38 (47%) of dogs under 10 kg. in weight, 15/27 (56%) of dogs 10.1 - 20 kg. in weight, 23/34 (68%) of dogs 20.1 - 30 kg. in weight, and 15/17 (88%) of dogs over 30 kg. in weight.

A similar increase of spondylosis with body weight is seen in the present study. In both dogs and vixens the Affection Index increases with body weight until an Affection Index of 50 in vixens, and 60 in dogs, is attained. Thereafter there is a marked decrease in body weight by 25%. Although there are very few animals with such a high Affection Index it seems clear that these animals have lost condition, and hence body weight, due to the debilitating effects of spondylosis. Such animals only represent 1.98% of the total sample of 252 adult animals, and it would seem fair to assume that these animals in poor condition have been selectively sampled, and so probably represent an even smaller proportion of the population. Foxes affected with spondylosis must, therefore, be able to survive all but the most severe levels of affection without any loss of condition.

Although it is impossible to study clinical signs in a wild population, such data are available for both man and several domestic animals. These studies agree in that badly affected animals may show no clinical signs, whereas other animals may exhibit such severe pain as to make walking impossible. Any symptons that do develop are usually referable to compression of the spinal cord and/or spinal nerves - Bailey & Casamajor (1911) showed that in man compression of the nerves and spinal cord may cause pain, paresthesia, local atrophy of muscles, and even paralysis may occur, and Parker & Adson (1925) described eight human patients with similar clinical signs. However the condition is often only discovered by accident - Garvin (1927) examined 2,090 patients over fifty years old for roentgenograms of the kidneys, ureters and bladder, and incidentally recorded spondylosis in 67% of the men and 40% of the women. Of these cases, Garvin found that 74% of the men and 61.5% of the women had no accompanying complaint of the various types of rheumatic and neuromuscular pains. Similarly Collins (1949) found that even very large osteophytes may cause no symptoms and that no clinical syndrome was known to be associated with the condition. Bick (1964) noted that in man spondylosis was apt to cause back pain during the fifth and sixth decades of life.

In dogs Glenney (1956) found that bone changes may cause stiffness, soreness and reduced motion in the hind legs, but seldom did he find sudden paralysis or acute pain. Archibald & Cawley (1966) noted that in dogs it was not uncommon for marked lameness to occur in one of the hind legs, or for the back to be slightly arched. However Morgan (1967) found that spondylosis was usually present without associated clinical signs.

Despite the slight variance between some of these observations, it seems that spondylosis usually only causes slight pain, this possibly increasing with age, although even well advanced spondylosis may elicit no clinical signs. In the fox no serious debility occurs until the condition is well advanced, when the animal loses weight. No other debilitating effects were noted.

6.5.9 Variations in the Vertebral Column

Variations in the number of vertebrae of closely related species can occur naturally, as was shown by Schultz & Straus (1945) in their detailed analysis of the number of vertebrae in Primates. Variations in number and morphology will also occur within a species.

Slijper (1946) described the mechanics of the mammalian spine, and noted that the point of greatest flexibility was at the diaphragmatic region - the tenth thoracic vertebrae in canids. It was therefore surprising to note 2/252 cases where the tenth and eleventh (anticlinal) thoracic vertebrae were fused by their spinal processes. Hildebrand (1954) noted the same in an Arctic fox, a Gray fox and a Domestic dog.

Flower (1885) noted that in the Carnivora the trunk vertebrae are nearly always 20 or 21 in number. He described two Red fox skeletons with the following arrangement of the vertebrae:-

$$C_7\ T_{13}\ L_7\ S_3\ Cy_{21}$$

$$C_7\ T_{14}\ L_6\ S_3\ Cy_{19}$$

The cervical vertebrae are invariably constant in number and the caudal vertebrae are quite variable, usually within the range 17 - 21.

Variations in the thoracolumbar vertebrae usually do not involve a variation in the total number of these vertebrae. Hildebrand (1954) quoted Miller, who only found one dog in 300 with 21 thoraco-lumbar vertebrae; Hildebrand also had one such specimen in his sample of 27 dogs. Sisson & Grossman (1955), also discussing the skeleton of the domestic dog, noted that the number of thoracic vertebrae may be twelve or fourteen, with or without compensatory change in the lumbar vertebrae. Shufeldt (1897-1901) also listed variations in the number of thoraco-lumbar vertebrae of canids.

More interesting is the variation in the sacrum, since this has a marked effect on the development of spondylosis. The present study found that 18.25% of the sacra showed some deviation from the normal pattern, and this confirms the data of Hildebrand (1954), who found that of 78 assorted canid sacra, 1 in 5 departed from the norm, and he described variations similar to those described here. Other authors all agree as to the variable character of the sacrum of canids.

Similar variations have been noted in the sacrum of other species. Bujalska (1961) described unilateral sacralisation of the last lumbar vertebra of Lepus europaeus, and Bujalska (1963) described bilateral sacralisation in the hare, but both these variations total only just over 2% of the sample. Roskosz (1962) noted over 30% sacralisation of the final lumbar vertebra in Bison bonasus.

There seems to be no significance to these skeletal variations, except as they affect the course of development of spondylosis deformans.

6.5.10 General Discussion

That a free-living animal population can exhibit such a high incidence of a debilitating disease is both unexpected and previously unrecorded. Ever since Darwin (1859) pronounced on the origin of species, and Spencer (1893) first introduced that much quoted ecological maxim "survival of the fittest", it has been assumed that animals struggle to survive, and that weak, sickly or injured animals are eliminated from the population by inter- or intraspecific competition. Although there are no other data on spondylosis deformans in a wild population, a consideration of the recorded instances of all forms of skeletal pathology is informative.

A simple state of affairs whereby injured and diseased animals are eliminated from the population is often said to occur with various species of mammal. For instance Dansie (1970) reports that in England muntjac (Muntiacus sp.) are naturally selected, dogs and cars removing the slow and less alert. Unfortunately he presents no data to substantiate this view. For deer populations, however, the principal of "survival of the fittest" has been neatly demonstrated by American studies of predation by wolves (Canis lupus) on larger cervids, two examples of which are discussed below.

Pimlott (1967) and Pimlott, Shannon & Kolenosky (1969) showed that in Ontario winter predation by wolves on White-tailed deer (Odocoileus virginianus) selected older animals. Of the wolf-killed deer, classes under 5 years of age included only 42% of the specimens, while those over 5 years of age contributed 58% of the total. Comparable figures for animals collected for research or killed by cars are 87% and 13%. Similarly Mech & Frenzel (1971) studied wolf predation on White-tailed deer in northeastern Minnesota. They showed that during the winter the wolves remove members of the prey population that are old, debilitated, or abnormal. It was also noted that these classes of deer represent such a small percentage of the population that they are seldom taken by human hunters.

In mammalian populations, these studies are the best examples of selective predation on debilitated animals. However the situation is unusual in that the ecological relationships involve only two species, with the wolves having no alternative winter food source, and they are in consequence entirely dependent upon the deer. In such a simple ecological situation strong selection pressures would be expected to operate against even relatively minor injuries to the prey species, as was demonstrated. In most ecological systems a greater number of species interact, so that one species is not entirely dependent on the other, and then such intense selection pressures need not necessarily operate against weak animals.

Recent work from more diversified ecological systems has shown that wild animals can and do survive serious injuries and pathological conditions. Gier (1968) has described skeletal injuries from coyotes (Canis latrans) in Kansas, and showed that animals can recover from severe injury without lasting weaknesses resulting, although Sperry (1939) has shown that "peg-leg" coyotes are less able to catch agile prey and eat more carrion and farm stock (mainly sheep and goats). Chapman & Chapman (1969a) examined the skeletons of 24 Fallow deer (Dama dama) killed by cars in Epping Forest; of these, 12 (50%) had degenerative lesions of various sorts, as a result of previous car accidents or gun-shot wounds. Spinage (1971) recorded two cases of pathological bone conditions in the impala (Aepyceros melampus) from Akagera National Park, and showed that both these animals demonstrated an ability to survive major injury and deformity in the wild. Spinage does not mention the sample size, but he does state that injured or deformed animals will always form a minority in normal populations, even though there may not necessarily be strong selection pressures operating against them other than those inherent in the evolution of the animal to start with. In the latter part of this assumption Spinage is almost certainly correct, but both Chapman & Chapman (1969a) and the present work have shown that injured or deformed animals do not necessarily form a minority of a population. When all the conditions in the adult foxes used in this study are completely catalogued, about half the population will exhibit one or more injuries or deformities.

Taylor (1971) examined the complete skeletons of 308 East African viverrids of nine genera and twelve species. Of these 308, 15% showed some sort of skeletal pathology. Depending on the species, the injuries were either attributed to cars or climbing accidents. Taylor commented that many injuries to viverrids seem to heal satisfactorily. He also rejected the hypothesis that an injured animal in the wild is soon eliminated from the population either because of inter-specific competition for food and/or territory, or by being preyed upon by another species.

Intra-specific competition is most important in a suburban fox population. The main source of "predation" on urban foxes is human, either in the form of direct control operations (shooting, gassing, or digging out of earths) or indirectly by means of cars and trains. In either case it would be logical to assume, but difficult to prove, that injured animals were less able to escape, and so form a bias in the sample. However loss of condition (body weight) was only seen in dog foxes with an Affection Index of more than 60, and in vixens with an Affection Index of more than 50; these totalled five animals from a sample of 252 (2%). Since only 2% of the population showed any signs of stress that could be attributed to spondylosis deformans, it is assumed that the sample was not markedly biased towards affected animals.

Other evidence also suggests that this sample bias towards injured or diseased animals is more theoretical than factual. Any animal that receives a serious injury, such as a fractured long bone, would be at its greatest disadvantage immediately after the injury. However, no animals were collected in such a condition, except those animals that suffered such severe injuries as to be rendered unconscious, or nearly so. Once the injury had healed, the animal would be far more capable of escaping "predation" than immediately after its accident, and so would be better able to survive.

This assumption that an injured animal cannot survive in a wild state has often been utilised by archaeologists to distinguish domestic animals from those from a wild population. Stecher & Goss (1961) examined the spines from 245 equine species, and found that ankylosing lesions were only found in domestic species. Zeuner (1963), when discussing features diagnostic of domestic animals, stated that "pathological conditions are often favoured and the withdrawal of animals from natural selection makes it possible to develop such characters in domesticated breeds". Zeuner further added that natural selection eliminates pathological types.

Berry (1969) discussed the value of all characters in the recognition of domesticated animals. He came to the important conclusion that it is not possible to recognise any traits which inevitably accompany domestication, and, even worse, most of the criteria by which domestication has been claimed to be recognizable may occur as a result of processes which have nothing to do with domestication.

The suggestion that features such as pathological conditions may arise as a result of processes other than domestication has been seriously overlooked by a number of workers. Harcourt (1967), in a study of osteo-arthritis in a Romano-British dog, argued that the degree of disability in this animal supported the view that it was a house dog, on the grounds that the condition is painful in the earlier stages and can be crippling, so that a village scavenger would have been unable to forage successfully and unable to hold its own in fights for food. However the degree of disability seen in Harcourt's specimen was no worse than that seen in several specimens collected in the present study, and they certainly survived without obvious serious handicap.

It may be argued that a suburban fox population is subject to less intense predation pressures than a more rural population, and that it is, in consequence, not surprising to find such a high incidence of skeletal anomalies. However, evidence from published life tables (Section 5) show that the life expectancy and rate of adult mortality of a suburban fox population is almost exactly the same as that of any other fox population. In many London Boroughs large numbers of foxes are destroyed each year, and since the sample came from these Boroughs one would expect the population to be subjected to a relatively high "predation" pressure.

Since it is obvious that the skeletal anomalies are not a feature of a sheltered existence, why suburban foxes should show such a high incidence needs some other explanation. The high incidence of fractures, nearly all attributable to car accidents, is not surprising, and such trauma does accentuate the degree of development of spondylosis deformans. Similarly a deficient diet may play some role in accentuating the disease. Glenney (1956) noted an early appearance of the disease in animals suffering from vitamin A deficiency. Similarly Wells (1964) noted that with an improvement in nutrition seen in ancient people there was a decline in the amount of arthritis.

It has proved impossible to determine the incidence of spondylosis deformans in rural foxes due to a lack of skeletal material, but examination of museum material has shown the disease to be absent in free-living Arctic foxes (Alopex lagopus)(although well-developed in specimens from Zoological Collections). Cross (1940) has noted the disease in a wild Timber wolf (Canis lupus lycaon), and Gadzhiev & Gadzhiev (1954) have shown the disease to be present in the fossil Binagadinsk wolf (Canis lupus apsheronicus).

Despite the contrary view of Fox (1939) it would appear that spondylosis is likely to be found in many species of wild canids, as well as in Domestic dogs. Such a high incidence in suburban foxes may not be a typical example, since the incidence of the disease has been increased by trauma, and possibly also dietary deficiencies. This can only be clarified by studying skeletal pathology in a rural population of Red foxes.

SECTION 7

THE FOOD OF SUBURBAN FOXES

7.1 INTRODUCTION

The Red fox is found throughout most of the world, due to both natural dispersion and to introductions by man. In consequence, the species is found in a wide variety of habitats, ranging from arctic tundra to Australian desert areas. To survive in such a variety of habitats, the animal must be adaptable and its feeding behaviour is important in this respect. The Red fox is widely recognised as an opportunistic feeder, eating anything that is available e.g. Arnold (1956), in his account of the Red fox in Michigan.

There have been some accounts of the ecological significance of the fox as a predator. It was found that under specialised conditions the fox can be a predator of considerable importance, particularly to aggregations of breeding animals. Kruuk (1964, 1972) showed that the fox was a major predator of a Black-headed gull (Larus ridibundus) colony, particularly under climatic conditions such as dark, stormy nights, which favour the predator and inhibit flight of the gulls. Bustard (1968) noted the fox to be a serious predator on nests of Sea turtles (Caretta caretta, Chelonia depressa and Chelonia mydas), the eggs being dug up just before hatching. Those eggs not eaten died of exposure. Norman (1971) studied fox predation on colonies of Short-tailed shearwaters (Puffinus tenuirostris), and found that fox predation was relatively unimportant unless no other vertebrate prey was present.

These general findings are also supported by extensive studies in Australia on the effects of foxes on lamb survival e. g. Alexander, et. al. (1967), who documented the development of a flock of Merino lambs. Predation on healthy lambs was not observed. Their results confirmed the Australian food study of McIntosh (1963), finding the fox to be an opportunist predator and a scavenger, utilising the most readily obtained food source.

A detailed review of the many analyses of Red fox food habits would not be relevant here, but a brief resumé of the main published works will be included on a continent by continent basis.

In America Scott (1941, 1943, 1947) studied fox feeding behaviour in Iowa. In his 1947 paper he compared fox feeding behaviour from two areas and showed that foxes would adapt their feeding in response to available food. This was demonstrated again by Errington & Scott (1945), who showed that during a drought period foxes readily modified their food habits to utilise a new food source, in this case muskrats (Ondatra zibethica) exposed by a dried-up marsh. The depredations of the foxes reduced about 25% of the trappers' income from the marsh.

Cook & Hamilton (1944) studied the ecological relationships of Red fox food in eastern New York. They found a marked seasonal variation in food habits, with mammals being most common in the winter and fruit most important in the autumn. Insects were taken to a limited extent in the summer and autumn, but birds were generally of little importance. Most of the food came from brush lots, fencerows and grassland, forests being of minor importance as a food source.

Latham (1950) reviewed the literature on fox food habits in the north-eastern United States; he listed all the published results (and some unpublished) but made no attempt to draw general conclusions on feeding trends.

Korschgen (1957, 1959) studied fox food habits in Missouri. He presented a detailed analysis of his results and (1959) a brief resumé of fox food studies in the Midwest and elsewhere, to complement the review of Latham for the northeast area. Most papers reviewed showed lagomorphs to be the principal food item, with small mammals second in importance. Other species of mammals and birds figured much less frequently.

There are many other smaller food studies on American foxes, all with the same general results. The only one of interest in the present context is that of Johnson (1970) for the Isle Royale National Park. Here again mammals were the most important food item with the Snowshoe hare (Lepus americanus) being the most important single item. Fruits were the main food in August and September. The area studied was of interest because it, like London, had relatively few mammalian prey species present. Johnson concluded that fox density was less than recorded elsewhere, and since the main prey species utilised on the mainland were not present on the island, "buffer species" (both plant and animal) were utilised to a greater extent. Johnson felt that the fox was not exploiting efficiently the food sources present, and that food was an important factor in limiting population growth.

In Australia the Red fox is an introduced species. Rolls (1969) described in detail how fox hounds were first used to hunt dingoes and macropods and then, when these species became fewer in numbers, foxes started to be introduced in the 1860s. Rolls alleged that the fox was an important predator of the many species of ground-nesting birds in Australia, and also of the native mammals.

McIntosh (1963) studied fox food habits in the Canberra district of Australia. He found the staple diet to be sheep carrion and rabbits, with invertebrates making up a large proportion of the diet during the warmer months and birds and cold-blooded vertebrates being of minor importance. He pointed out that there was no evidence to support allegations that foxes are a menace to ground-nesting birds.

McIntosh's study area contained few native mammal species. Martensz (1971) studied fox food in an arid area of New South Wales, where such species were more common. He found a greater variety of reptile and mammal species in the fox stomach contents, but even here the main food was carrion, in this case the remains of kangaroos shot by a professional shooter.

Coman (1973) studied fox food habits in Victoria, and found very similar results to those already described. He found the main food items to be rabbits, sheep carrion and mice, with lesser amounts of native mammals, birds, cold-blooded vertebrates, invertebrates and plant material. Coman also demonstrated a seasonal and regional variation in food habits, but was unable to draw any conclusions on the significance of fox predation on native wildlife.

There have been several food studies in Eurasia, one of the earliest being that of Baranovskaya & Kolosov (1935), who described the food habits of the fox in Russia. More recently Petrov (1967) studied the food of foxes (Vulpes vulpes karagon) in Middle Asia (west Tian-Shan). He presented food habits analyses for three separate years, and found that vertebrates were of minor importance in the diet, mammals and birds being eaten seldom. The main food items were insects, wild fruits and berries.

Ryszkowski, Wagner, Goszczyński & Truszkowski (1971) studied the effects of a variety of carnivores, including foxes, as predators of small mammals in forests and cultivated fields in Poland. They found that the intensity of predation on rodent populations was very high and in fact more Field voles (Microtus arvalis) were eaten than had been estimated to be present! Rzebik - Kowalska (1972) studied the food habits of foxes in Poland, finding that mammals were of greatest importance as food items, with birds coming second. The results supported the general findings of the predation study, since the greatest single food item was voles, mainly Microtus, and the most important avian prey item was the

Domestic hen. Similarly, Goszczyński (1974) studied the food of foxes in Poland. He found that small rodents dominated the diet of foxes, and that of these 93.1% were Microtus arvalis. The availability of voles was a factor deciding the diet of foxes. Hares were of secondary importance, with Roe deer and birds as supplementary constituents.

In Europe Lund (1962) studied the food habits of the fox in Norway, an area which lacks wild rabbits. His results, however, were not markedly different from those recorded in other countries, rodents, particularly Microtinae, forming the bulk of the food. Murids were of lesser importance. Birds constituted 30% of the warm-blooded prey, particularly the families Turdidae and Tetraonidae. Berries and fruits were of importance in the autumn.

Englund (1965a, 1965b, 1969) studied the food of foxes in Sweden. His detailed analyses yielded results very similar to those of Lund, with Microtinae being the most important single food item. Englund also showed that small rodents were consumed to a greater extent when the supply of small rodents increased, and at the same time other kinds of food declined in importance. In his study on Gotland, where voles are absent, Englund (1965b) showed that when the rabbit population declined to 1/20th. as a result of myxomatosis, the precentage of stomachs containing rabbits declined to a half, hares, mice and pheasants compensating for the decrease of rabbits in the foxes' diet. Studying the food of fox cubs Englund (1969) showed that where the small rodents constitute the staple food, hares occur more frequently in the stomach of smaller cubs, these large prey items being brought back to the earth by the adults. Englund documented a series of changes in food habits during the development of the cubs.

Fairley (1965, 1966, 1970) has studied the food of the fox in Ireland. In his first two papers he compared the food of foxes in Co. Down at a time of high rabbit populations with the food of foxes in Cos. Down and Antrim after a reduction in the rabbit population due to myxomatosis. He found a marked reduction in the number of rabbits, associated with an increase in the percentage occurrence of Brown rats. There was no change in the number of woodmice. Fairley suggested that rats and not mice fulfil the role played by Microtinae in the majority of food studies.

Fairley (1970) presented a detailed analysis of the food of foxes in north-east Ireland. This showed mammals to be the most important class of food items, with lagomorphs of greatest importance and rats coming second. Galliformes were the most important bird food item recorded. However Fairley admitted that he did not bother to search his samples for chaetae, and since the present work suggests that this introduces a major bias to his results these must be viewed with caution.

In Scotland there have only been superficial food studies. Lockie (1956) studied the food of foxes before and after myxomatosis, finding a decline in the importance of rabbits and an increase in the importance of voles and mice. In Wester Ross Lockie (1964) found voles, sheep and deer carrion to be of importance in the foxes' diet. Similarly Douglas (1965) in his study of foxes shot near Braemar during April and May found deer carrion to be of major importance.

In England there have been surprisingly few Red fox food studies, although several notes reporting unusual food items have been published. Southern & Watson (1941) presented an analysis based on 40 stomachs and 18 faecal pellets, all collected during the summer. They found the commonest food items to be rabbits, sheep, small birds and insects in that order, with sheep and small mammals being taken more frequently in hill districts of Wales than in the Midlands.

Lever (1959) presented a more detailed analysis, based on a much larger sample (420 stomachs and 123 scats). His study was made after the advent of myxomatosis, and found that rabbits had declined from 50% occurrence, as recorded by Southern & Watson, to 20%. He found that Microtus agrestis had replaced the rabbit in importance, voles occurring in over 40% of lowland stomachs and 55% of stomachs from hill areas.

Rattus norvegicus was the next most frequent rodent. Birds featured more commonly in lowland areas (63%) than in hill areas (40%), game and poultry representing 1/3rd - 1/2 of all birds eaten.

Burrows (1968) presented a detailed analysis of fox food habits in lowland Gloucestershire. He found small rodents, mainly Field voles, and rabbits, to be major food items, with insects and fruit of seasonal importance. He also showed the importance of earthworms in the diet of foxes. Later Jefferies (1974) discussed the importance of earthworms in the diet of foxes (without reference to the work of Burrows) based on a single animal. Jefferies noted that the earthworms most likely to occur in a foxes diet are Lumbricus terrestris since "both feeding and copulation occur on the surface of the soil whereas for all other species these occur almost invariably below the surface".

There have been no quantifiable studies on the food habits of suburban foxes. Teagle (1967) presented a detailed discussion of fox food habits in rural areas but very little of this was directly relevant to suburbia. He noted that suburban foxes were known to feed on rats, that predation on cats was probably exaggerated, and that many foxes feed on household waste, but he admitted to having no data to support these assumptions. Beames (1972) presented no data, merely repeating the views of Teagle, also making a few unsupported remarks relating to suspected predation on pets. Such remarks are widely repeated by "popular" authors e.g. Mabey (1973).

Beck (1973) reported on the food habits of free-ranging dogs in Baltimore, but presented no quantified data. He noted that urban dogs find food chiefly in garbage and human hand-outs, but that some active predation may occur on rats in alleys and on birds in urban wooded areas.

A quantified study on the food habits of suburban foxes is obviously desirable since heavy predation on pets and ornamental waterfowl is of economic importance, and heavy predation on small passerines is of ecological and aesthetic importance. An ideal food study should also document the availability of food items, to document fox food habits in relation to food availability. However attempts to achieve this for suburbia proved impossible due to the lack of free access to the study areas. Fortunately the bird populations are very well documented - the London Natural History Society (1964) listed the birds of the London area, with some information on abundance, and Simms (1975) has presented a very detailed analysis of the distribution of birds in London in relation to the various habitats available. The mammals are less well recorded, but some data has been drawn from the Annual Mammal Reports in the London Naturalist, and the survey of small mammals by Corke & Harris (1972).

7.2 METHODS

There are five possible means of determining the food habits of suburban foxes:-

a) direct behavioural observations

b) collecting reports on damage by foxes

c) scat analysis

d) stomach contents analysis

e) recording den litter.

Each technique has its own inherent advantages and disadvantages, as follows:

a) Direct behavioural observations are of limited use. To be of value, long periods of continuous observation on particular animals are desirable, which is rarely possible in an urban environment. Even when this has been achieved it has proved impossible to identify the small food items picked up by foxes, and since most of these observations have been of foxes "hunting" playing fields and parks in the early morning it was impossible to determine visually what the foxes were collecting.

Obviously all the information collected is biased towards the larger food items, and since this technique has yielded no new data it will not be considered further.

b) Reports on damage by foxes are interesting from the economic point of view, but of little value in a quantified food study. In Boroughs where the Council offers a fox control service, many of the complaints received refer to the killing of pets (cats, rabbits, guinea pigs, bantams and hens) and ornamental water fowl, or to digging up lawns, either for some invertebrate food or in response to an application of blood fertiliser.

This technique again obviously biases any results to the larger food sources, and also gives a false impression of the importance of pet animals in the diet of suburban foxes.

c) Scat analysis was not a particularly useful technique, since in suburbia it proved impossible to regularly collect scats, except those of cubs around earths, and even then the scats often contain no recognisable food items, making it difficult to be sure that they were vulpine in origin.

Scat analysis was extensively utilised with great success by Scott (1941, 1943, 1947) in his analysis of fox feeding behaviour in Iowa. However he noted that "fecal analysis is uncertain when easily digested foods or those lacking indigestible elements are eaten, and in some instances the utility of the technique may depend on whether or not animals consume significant amounts of such foods".

This proved to be the major draw-back to scat analysis in suburban foxes. A large sample of rectal contents was analysed and compared with the results obtained for stomach content analysis. It was found that the soft foods were unrecognizable in the rectal contents, so biasing the data towards food items with indigestible remains. For a fuller discussion of the problems inherent in scat analysis see Lockie (1959). In view of this bias the technique was abandoned for suburban foxes.

Goszczyński (1974) utilised scat analysis to study the diet of foxes at Turew, Poland, where he showed the principal prey items to be small rodents, hares, birds and Roe deer, with occasional occurrences of insectivores, plants and insects. Although these were the only prey items found in the scats, Goszczyński seems to have made no effort to ensure that no soft food items were ingested. In view of the large areas of meadow in the study area it seems strange that he failed to record earthworms in the diet. Murie (1946) showed that the number of rabbit-sized animals could be judged accurately from coyote scats, but small animals could be considerably underestimated.

d) Stomach content analysis is the most useful technique for fox food habit analysis. Amongst many others, this technique has been used extensively by Englund (1965a, 1965b, 1969) to study the food of foxes in Sweden.

In the present study stomachs were removed as soon after death as possible and preserved in 70% ethyl alcohol. The stomachs were opened in the laboratory, the contents weighed, and a series of smears examined for the presence of chaetae. The contents were then washed through a fine sieve, particularly fatty stomach contents being washed in warm water with a small amount of detergent (Fairley 1970).

How to quantify the various food items present is a difficult matter. Englund (1965a) discussed the various methods for quantifying the composition of the food, and eventually decided to present his data as frequency occurrence, the frequencies of the different kinds of prey being stated in relation to the number of stomachs with contents. Korschgen (1957, 1959) presented his data as percentage occurrence and percentage volume, and with most food items the results obtained were very similar.

Obviously some method of quantifying the relative importance of each food item is desirable. However in the present study percentage volume and percentage weight would be impracticable since large amounts of soft, readily digested food are ingested. Most foxes were shot in the middle of the day, when all soft food items are largely digested. Particularly important in this respect are earthworms, which were only represented in stomach contents by chaetae (see results for discussion), and cannot be recorded by weight or volume. In view of these difficulties, the technique of Southern & Watson (1941) was used, whereby each food item was given an abundance rating of 1 - 5, as follows:-

1 indicates a trace
2 indicates a small amount
3 indicates a moderate amount
4 indicates a large amount
5 indicates stomach distended with that particular food.

These scales have to be interpreted liberally, since a rating of "5" for chaetae would indicate that the stomach had been distended with worms, but at the time of collection only vast numbers of chaetae (and earth) were present. Results are presented as a percentage of the total abundance rating.

Mammalian hairs were identified using the keys of Appleyard (1960) and Day (1966), identification being to the species level using cuticular scale patterns and cross-sections, these sections being prepared on a Wira Hardy Microtome. Bird feathers could normally only be identified to the order level, using the key of Day (1966). Insect remains were badly chewed, but these were usually identifiable to the generic level, and often to the species.

To examine the food of suburban foxes, only stomachs from foxes killed in truly suburban habitats were used (gardens, allotments, factories, waste ground, etc.). Stomachs from specimens killed in the Royal Parks and larger open spaces were analysed, but here very different food items were available to the foxes, and so these results are not included since they obscure the more interesting details on food habits in suburbia. Similarly, stomachs from all animals caught in baited box traps were discarded - these usually only contained the bait used in the trap.

The monthly distribution of stomachs included in this analysis is shown in Table 35.

e) Recording den litter is a useful technique if its limitations are fully appreciated. Any small food items will be under-recorded, particularly small birds and mammals, since these will be eaten whole; large food items will be eaten over a period of a couple of days, and the indigestible remains will be prevalent for a long period of time. This is particularly true for the large meat bones found outside suburban fox earths. The bones of mammalian and avian prey items do not persist long since, being more delicate, they are eaten with the carcass, thereby tending to exaggerate the importance of meat bones as a food item. Sometimes mammalian food items,

TABLE 35

MONTHLY DISTRIBUTION OF FOX STOMACHS UTILISED IN FOOD HABITS ANALYSIS, THE NUMBER IN BRACKETS BEING THE NUMBER OF EMPTY STOMACHS

Month	Adults	Cubs
January	10 (3)	
February	38 (10)	
March	15 (9)	
April	12 (3)	4 (2)
May	14 (2)	47 (5)
June	7 (2)	24 (3)
July	4 (1)	11 (3)
August	7 (4)	11 (4)
September	6 (2)	9 (3)
October	9 (2)	
November	32 (9)	
December	11 (1)	
Totals	165 (48)	106 (20)

Total of 271 animals, of which 203 (74.91%) had food remains in their stomach.

particularly hedgehogs, are eaten with the back skin left intact, completely cleaned of meat. This then dries and persists for some time as a play item.

Thus at any particular visit to an occupied earth, small food items are virtually non-existent, meat bones accumulated over a long period abound, and remains of the recently killed larger birds and mammals persist.

The advantage of the technique is that it allows accurate identification of the avian prey items (e.g. the relative importance of wood and feral pigeons), it may allow one to determine whether a particular mammal was actually caught or found as a road casualty; it also allows one to determine the sources of the assorted bone fragments and pieces of fat found in the stomach contents.

Den litter studies therefore complement an examination of stomach contents. Considering the advantages that the technique offers, it is a mode of study that has been somewhat neglected for the Red fox, one of the few recent examples being that of Coman (1972) in Victoria, Australia.

7.3 RESULTS

7.3.1 Stomach Contents

The results of the stomach contents analysis are shown in Figures 31 and 32, and in Tables 36 to 44. A large proportion of the stomach contents consisted of non-food items (27.1% in adults, 27.5% in cubs). Some of these items were obviously ingested co-incidentally while feeding (e.g. large quantities of earth ingested while feeding on earthworms), while other items, such as ornamental dwarf conifers (22

FIGURE 31 MONTHLY VARIATION IN ADULT STOMACH CONTENTS. PERCENTAGE BASED ON THE TOTAL ABUNDANCE RATING FOR EACH MONTH

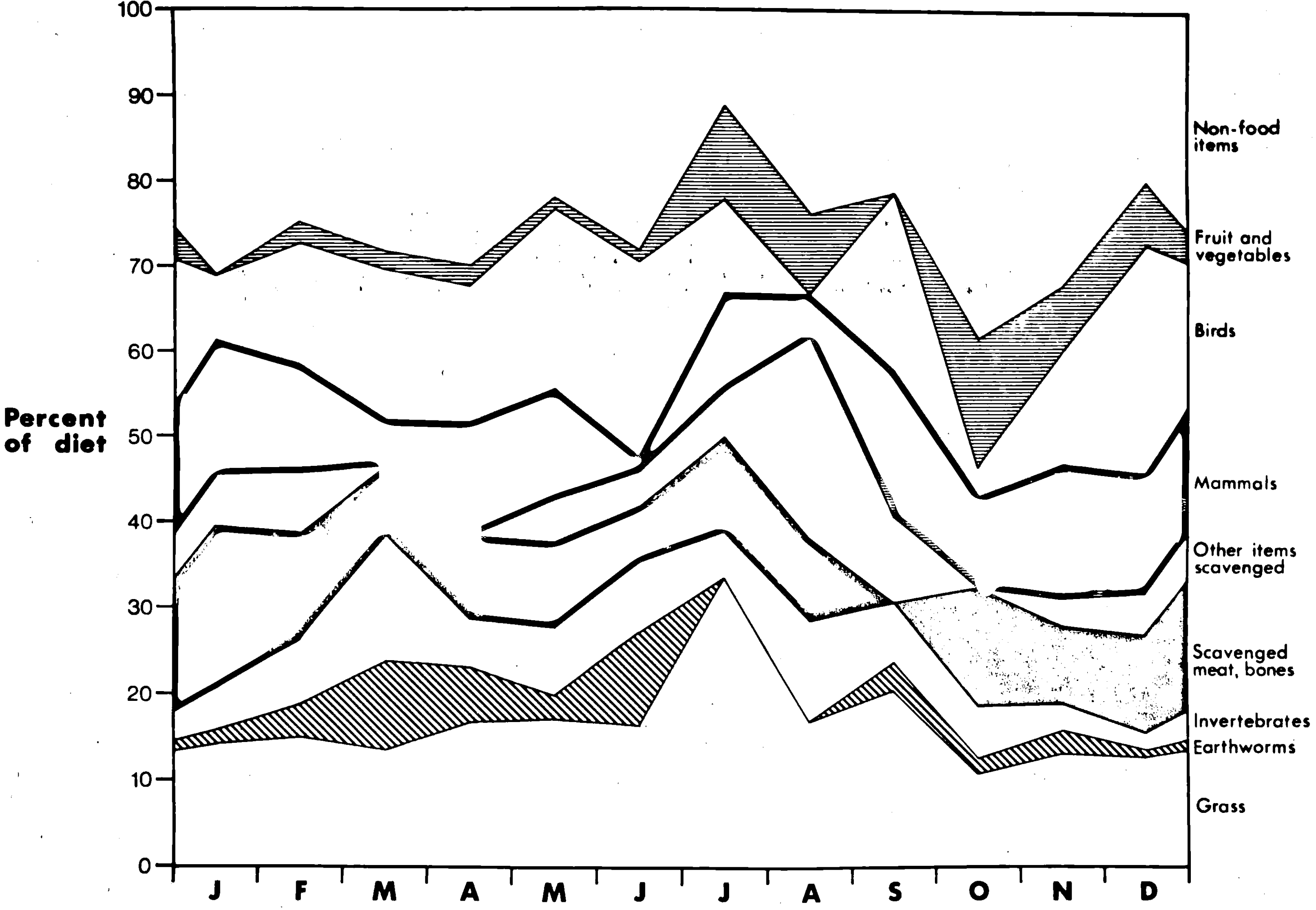
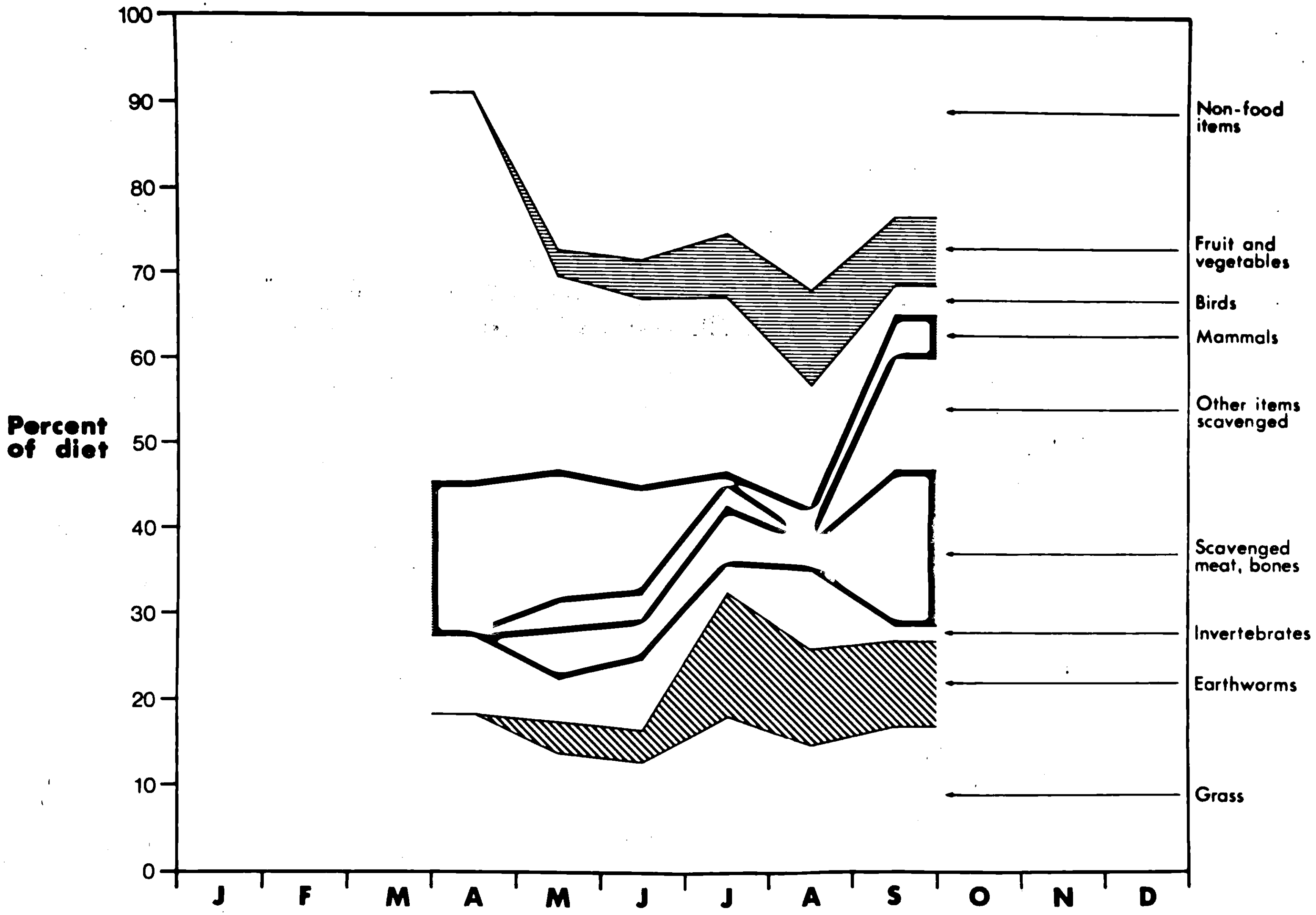

Percent of diet
100
90
80
70
60
50
40
30
20
10
0
J
F
M
A
M
J
J
A
S
O
N
D
Non-food items
Fruit and vegetables
Birds
Mammals
Other items scavenged
Scavenged meat, bones
Invertebrates
Earthworms
Grass

FIGURE 32 MONTHLY VARIATION IN CUB STOMACH CONTENTS. PERCENTAGE BASED ON THE TOTAL ABUNDANCE RATING FOR EACH MONTH


Percent of diet
100
90
80
70
60
50
40
30
20
10
0
J
F
M
A
M
J
J
A
S
O
N
D
Non-food items
Fruit and vegetables
Birds
Mammals
Other items scavenged
Scavenged meat, bones
Invertebrates
Earthworms
Grass

occurrences) seem to have been specifically ingested. Also, many of the dead leaves were dead Taxus leaves, although why foxes should have selectively eaten conifers is unknown. Only a small percentage of the diet is obtained by scavenging (15.6% in adults, 9.2% in cubs), the bulk of the diet being obtained by predation on mammals and birds (27.4% in adults, 32.0% in cubs). In both cases birds were of greater importance than mammals in the diet, contributing to the diet in the ratio of 1.3 : 1 in adults and 1.8 : 1 in cubs.

Seasonal variations in the adult diet are not very pronounced. Earthworms were at their most important in March, as were insects, when large numbers of noctuid caterpillars were taken. There was an increased predation on Passeriformes during May and June, when most of the specimens eaten were juveniles. Fruit and vegetables were of greatest importance in the late summer and autumn, but windfall apples can be found in the stomachs of foxes killed at most times of the year, although these may be very dried and shrivelled. Both scavenging and predation were maintained at a fairly constant level throughout the year. There was some seasonal variation inthe type of food scavenged - during the winter food put out for the birds was of particular importance e.g. sultanas, chopped nuts, and orange peel.

Seasonal trends are more pronounced in cub stomach contents. For the months of April, May and June the cubs were being fed by their parents, and most of the food consisted of mammals and birds. As the cubs started to learn to feed themselves in July, August and September mammals became infrequent, although quite a few birds were still eaten (mainly easily caught Passeriformes). At this time earthworms became much more important, and there was an increase in the occurrence of fruit and vegetables. Particularly in September, when the cubs became independent, scavenging was the major source of food (31.6% of the total stomach contents). There was some monthly variation in the species of insects eaten - Lucanus cervus was common in June, carabids in July, but at no time was predation on insects heavy, and they were of lesser importance than earthworms in the diet of suburban fox cubs.

TABLE 36

STOMACH CONTENTS OF ADULT SUBURBAN FOXES. FIGURES ARE PERCENTAGE OF TOTAL ABUNDANCE RATING FOR THAT MONTH

	J	F	M	A	M	J	J	A	S	O	N	D	Total
Grass	14.1	14.9	13.5	16.7	17.0	16.2	33.3	16.6	20.7	10.8	13.1	12.4	14.9
Earthworms	1.6	4.0	10.4	6.3	2.8	10.8	0	0	3.5	1.5	2.6	1.0	4.0
Other invertebrates	4.7	7.3	14.6	5.6	7.8	8.1	5.6	11.9	6.9	6.2	3.0	1.9	6.4
Scavenged meat, bones, fat.	18.8	12.6	8.3	9.5	9.9	6.8	11.1	9.5	0	13.8	9.3	11.4	10.6
Other items scavenged	6.3	6.9	0	3.2	5.0	4.1	5.6	23.8	10.3	0	3.0	4.8	5.0
Mammals	15.6	12.6	5.2	10.3	12.8	1.4	11.1	4.8	17.2	10.8	15.7	14.3	11.9
Birds	7.8	14.2	17.7	15.9	21.3	23.0	11.1	0	20.7	3.1	13.4	26.6	15.5
Fruit and vegetables	0	2.6	2.1	2.4	1.4	1.4	11.1	9.5	0	15.4	7.8	7.6	4.6
Non-food items	31.1	24.9	28.2	30.1	22.0	28.2	11.1	23.9	20.7	38.4	32.1	20.0	27.1
Total %	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

TABLE 37

STOMACH CONTENTS OF SUBURBAN FOX CUBS. FIGURES ARE PERCENTAGE OF TOTAL ABUNDANCE RATING FOR THAT MONTH

	J	F	M	A	M	J	J	A	S	O	N	D	Total
Grass				18.2	13.6	12.4	17.8	14.4	16.7				14.0
Earthworms				0	3.8	3.9	14.4	11.3	10.0				6.1
Other invertebrates				9.1	4.9	8.1	3.4	9.3	1.7				6.0
Scavenged meat bones, fat.				0	6.0	4.9	6.8	3.1	18.3				6.1
Other items scavenged				0	2.9	2.9	2.5	0	13.3				3.1
Mammals				18.2	15.6	12.7	1.7	4.1	5.0				11.5
Birds				45.5	22.5	21.8	20.3	14.4	3.3				20.5
Fruit and vegetables				0	3.3	4.6	7.6	11.3	8.3				5.2
Non-food items				9.0	27.4	28.7	25.5	32.1	23.4				27.5
Total %				100.0	100.0	100.0	100.0	100.0	100.0				100.0

TABLE 38

INSECTS FOUND IN SUBURBAN FOX STOMACHS, THE CLASSIFICATION USED BEING THAT OF KLOET & HINCKS (1945). ALL SPECIMENS ARE ADULTS EXCEPT WHERE OTHERWISE STATED.

		Number of Occurrences	Number of Specimens
Orthoptera			
Acrididae		2	2
Omocestus viridulus (Linnaeus 1758)		1	1
Dermaptera			
Forficulidae	- nymphs	1	1
Forficula auricularia Linnaeus 1758		4	4
Trichoptera		1	2
Lepidoptera	- adults	4	6
	larvae	25	58
Noctuidae	- adults	1	1
	larvae	4	6
	probable noctuid larvae	4	119
Coleoptera			
Carabidae	- adults	4	4
	larvae	3	3
Carabus sp. Linnaeus 1758	- adults	1	1
	larvae	1	1
C. granulatus Linnaeus 1758		1	1
C. nemoralis O.F. Mueller 1764		2	5
C. violaceus Linnaeus 1758		5	9
Nebria sp. Latreille 1802		1	1
Harpalus sp. Latreille 1802		1	1
Amara sp. Samouelle 1819		1	1
Pterostichus sp. Stephens 1827		3	3
P. melanaria (Illiger 1798)		1	4
P. madida (Fabricius 1775)		1	3
Hydrophilidae			
Cercyon sp. Leach 1817		1	1
Staphylinidae		2	2
Elateridae		1	1
Lucanidae			
Lucanus cervus (Linnaeus 1758)		7	7
Hymenoptera			
Formicidae			
Lasius niger (Linnaeus 1758)		12	71
Vespidae			
Vespa sp. Linnaeus 1758		1	1
Apidae			
Apis sp. Linnaeus 1758		3	3
Diptera	- unidentified larvae	14	154
	unidentified pupae	1	2
Tipulidae	- larvae	4	5
Bibionidae	- larvae	1	1
Scatopsidae	- larvae	1	52
Calliphoridae	- adults	1	1
Muscidae	- adults	1	1
Fannia sp. Robineau-Desvoidy 1830	- larvae	2	10
Siphonaptera			
Pulicidae			
Archaeopsylla erinacei (Bouché 1835)		1	9

TABLE 39

ARTHROPODS OTHER THAN INSECTS FOUND IN SUBURBAN FOX STOMACHS

	Number of Occurrences	Number of Specimens
Chilopoda		
Geophilomorpha		
Geophilus sp.	1	1
Lithobius sp.	1	2
Crustacea		
Isopoda		
Porcellio sp.	1	1

TABLE 40

SCAVENGED FOOD ITEMS FOUND IN SUBURBAN FOX STOMACHS

	Number of Occurrences.
Scavenged meat items	
Assorted mammalian & avian meat, bones, fat	78
Fish bones, including tinned salmon	3
Bacon rinds	1
Other scavenged food items	
Potato peelings	23
Sultanas	19
Bread	4
Orange peel and pips	4
Chopped walnut	1
Tinned carrot and carrot peelings	4
Mixed dried fruit	1
Cloves	1
Seeds, corn, etc., probably derived from bird guts	7

TABLE 41

MAMMALIAN FOOD ITEMS FOUND IN SUBURBAN FOX STOMACHS

	Number of Occurrences	Number of Specimens
Domestic pets		
Oryctolagus cuniculus	12	12
Felis catus	6	6
Cavia porcellus	1	1
Wild mammals		
Microtus agrestis	29	40
Rattus norvegicus	18	18
Sciurus carolinensis	12	12
Apodemus sylvaticus	8	8
Oryctolagus cuniculus	7	7
Vulpes vulpes	6	6
Erinaceus europaeus	3	3
Clethrionomys glareolus	2	2
Mus musculus	1	1
Meles meles	1	1

TABLE 42

AVIAN FOOD ITEMS FOUND IN SUBURBAN FOX STOMACHS

	Number of Occurrences	Number of Specimens
Domestic pets and ornamental waterfowl		
Galliformes		
Chickens of various breeds	22	22
Anseriformes		
Adults	1	1
Ducklings	1	2
Eggshells	1	1
Psittaciformes		
Melopsittacus undulatus	1	1 or 2
Wild birds		
Passeriformes		
Unidentified passeriformes	73	78
Passer sp.	9	9
Turdus merula	7	7
Sturnus vulgaris	1	1
Erithacus rubecula	1	1
Columbiformes		
Unidentified species	22	22
Galliformes		
Unidentified species (not hens)	1	1
Unidentified birds, presumed to be wild	2	2

TABLE 43

FRUIT AND VEGETABLE FOOD ITEMS FOUND IN SUBURBAN FOX STOMACHS

	Number of Occurrences
Apple	31
Pear	8
Bulbs	6
Tomatoes	5
Cherries	4
Hawthorn fruits	3
Plums	3
Gooseberries	3
Peas	3
Beans	2
Cabbage	2
Fresh carrots	1
Melons	1
Peaches	1

TABLE 44

NON-FOOD ITEMS FOUND IN SUBURBAN FOX STOMACHS

	Number of Occurrences
Moss	42
Quantities of earth	59
Dead leaves	131
Live leaves	25
Pieces ornamental dwarf conifer	22
Leather straps, etc.	5
Paper and silver paper	50
Pieces of string	10
Pieces of cellophane and polythene	11
Pieces twigs, bark, wood	63
Fox fur from grooming, etc.	37
Seeds trees and various plants	2
Dead flowerheads	17
Small stones	12
Pieces walnut shell	4
Pieces of plastic	3
Spines and thorns	6
Shoelaces	1
Pieces of wire	1
Pieces of china	1
Pieces of linoleum	1
Pieces of brick	1
Pieces of plant stem	2
Pieces of unidentified artificial fibre	2

7.3.2 Siting of Fox Earths

Many fox earths are to be found in London, but the majority of these were never observed to contain cubs, and were only utilised by adults during severe weather or when being pursued. Every raised garden shed is a potential earth, although the same few sheds are used time and again for rearing cubs (some earths are known to have contained cubs every year for a quarter of a century).

A list of the earths that were found to contain cubs is shown in Table 45, the majority of such sites being under small garden sheds. In such situations the cubs are reared above ground, under the floor of the shed, or actually underground in holes dug under the shed.

7.3.3 Den Litter

The majority of suburban fox cubs are born at the end of March or beginning of April, and food remains start to accumulate from the end of April, when the cubs are three to four weeks old. The earths are then used regularly until the end of June, when the cubs start to lie above ground, either on waste ground or under raised buildings, in the vicinity of the natal earth. This move is precipitated by hot weather. Cubs can occasionally be found in earths later in the year. Food is still brought to these lying-up areas by the parents, and any such food items recorded were grouped with the den litter.

In total, outside 97 earths and in 4 play areas, 508 food items, 81 play items and the remains of 12 dead foxes were recorded. These dead foxes were usually cubs of the previous year that had been gassed, their bones being turned out by the current occupants.

A full list of the various food and play items is shown in Tables 46 - 50. Each meat bone was listed separately, although in very fresh specimens these may have been joined (e.g. radius and ulna), and occasionally even complete fore-legs of e.g. lamb were found. However

TABLE 45

SITING OF SUBURBAN FOX EARTHS WHICH CONTAINED CUBS

Situation	Number	Percentage
Under garden sheds with raised floors	36	37.1
Under concrete floors of garages, outbuildings, and raised floors of summer-houses, portable huts, etc.	10	10.3
In air-raid shelters	1	1.0
In drains	1	1.0
In banks of earth e.g. at bottom of gardens, railway embankments, etc.	29	29.9
In flat ground	9	9.3
In flower beds, rockeries, etc.	6	6.2
In compost heaps, piles of rubbish, wood piles, etc.	5	5.2
Total	97	100.0

TABLE 46

MAMMALIAN PREY ITEMS FOUND OUTSIDE SUBURBAN FOX EARTHS

Prey Item	Number
Domestic pets	
Oryctolagus cuniculus	5
Felis catus	2
Sus scrofa (entire piglets)	4
Mustela furo	2
Wild mammals	
Rattus norvegicus	5
Sciurus carolinensis	4
Oryctolagus cuniculus	1
- only bones, either pet or wild	2
Erinaceus europaeus	3
Vulpes vulpes	
cannibalised cubs	3
bones only, presumed not to have been cannibalised	12
Total prey items (excluding fox bones)	31

TABLE 47

AVIAN PREY ITEMS FOUND OUTSIDE SUBURBAN FOX EARTHS

Prey Item	Number
Domestic pets and ornamental waterfowl	
Galliformes	
Chickens of various breeds	16
Chickens - probably scavenged	2
Chickens - bones of unknown source	28
Turkeys - bones of unknown source	6
Anseriformes	
Goose - bones of unknown source	1
Anas platyrhynchos	2
Cygnus olor (cygnet)	1
Ralliformes	
Gallinula chloropus	1
Columbiformes	
Columba livia - racing pigeon	1
Psittaciformes	
Melopsittacus undulatus	1
Wild birds	
Passeriformes	
Unidentified passeriformes	7
Passer sp.	12
Turdus sp. (thrushes)	9
Turdus merula	35
Sturnus vulgaris	2
Motacilla alba	1
Corvus frugilegus	2
Charadriiformes	
Larus marinus	1
Columbiformes	
Columba sp.	8
Columba palumbus	2
Columba livia	28
Birds Eggs	
Pigeon eggs	1
Hen eggs	1
Total prey items	168

TABLE 48

SCAVENGED MAMMALIAN MEAT BONES FOUND OUTSIDE SUBURBAN FOX EARTHS

Food Item	Number
Pork and bacon bones	
Scapula	8
Humerus	20
Radius	13
Ulna	17
Pelvis	8
Femur	9
Tibia	8
Fibula	2
Carpal and tarsal bones	1
Vertebrae	2
Skull	1
Lower jaw	1
Entire trotters	1
Total pork and bacon bones	91
Lamb and mutton bones	
Scapula	13
Humerus	7
Radius	5
Ulna	7
Pelvis	12
Femur	19
Tibia	22
Carpal and tarsal bones	6
Vertebrae	8
Total lamb and mutton bones	99
Beef and calf bones	
Scapula	2
Humerus	4
Radius	2
Ulna	3
Pelvis	1
Femur	2
Tibia	1
Sacrum (half)	1
Vertebrae - sawn in half	13
Ribs	21
Total beef and calf bones	50
Other scavenged meat bones	
Unidentified bones	18
Half vertebrae from chops	13
Heads of ribs from chops and cutlets	16
Lump fresh ribcage	1
Total scavenged meat bones	288

TABLE 49

OTHER SCAVENGED FOOD ITEMS FOUND OUTSIDE SUBURBAN FOX EARTHS

Food Item	Number
Slices of white bread	5
Lumps of white bread	9
Sandwiches	1
Peanuts - unsalted	1
Potato peelings	1
Bacon rind and skin	2
Lumps of fat	2
Total food items	21

TABLE 50

PLAY ITEMS FOUND OUTSIDE SUBURBAN FOX EARTHS

Play Item	Number
Golf balls	5
Tennis balls	10
Cricket balls	1
Rubber balls	4
Leather straps	1
Half-coconuts	1
Rubber household gloves	1
Dog chews - moccasin-shape	1
Nylons	1
Fish and chip papers	18
Col. Sanders Kentucky Fried Chicken papers	1
Sandwich bags	17
Plastic bags	13
Loaf wrappers	2
Soft-margarine containers	1
Meat pie wrappers	1
Milk carton	1
Wine wrapper	1
Cigar packets	1
Total play items	81

as they are eaten they readily separate into the individual bones, and this had already occurred in most cases. As a result 288 meat bones represents fewer items actually collected by the fox, but since in most cases the bones had already been separated it was impossible to estimate how many separate food items were involved.

7.4 DISCUSSION

7.4.1 Stomach Contents

Korschgen (1971) presented a detailed discussion on the needs for competent food studies by wildlife biologists. He noted that the primary purpose of food-habits investigations is to learn which foods are utilised by wild animals, and how, when and where such foods are obtained. Korschgen also discussed the difficulty in determining what is an adequate sample size. This must be determined by noting the extent of changes that occur when additional units are analysed and added during the study. Korschgen presented three criteria used to judge the extent of such changes with an increase in sample size:-

i) uniformity of volumetric percentages is maintained

ii) the rate of appearance of important new food items

iii) overall uniform percentages of individual food items.

Sample size can only be considered large enough when new samples add no significant new information to that obtained from previous samples. In the present study the last fifty stomachs yielded only one new food item (Cavia porcellus), which is not of major importance in the food habits of suburban foxes, and so by Korschgen's criteria the overall sample size is adequate, although for the summer months the adult sample size is low and more information for these months is desirable.

One other criterion of Korschgen was that samples should be collected over a minimum period of two years; this has been done in the present study.

Most of the foxes used in this study were shot between 10.00 a.m. and 2.00 p.m. Behavioural studies suggest that the majority of the feeding (and activity generally) occurs between 10.00 p.m. and 5.00 a.m. As a result at the time of death soft foods would be more completely digested than harder food items - hence most of the bird and mammal remains consisted mainly of skin, fur and feathers, with a few splintered bones. Also, since most non-food items were hard and indigestible the large volume of the stomach contents that they constitute is an artefact resulting from the time of death. Observations suggest that most earthworms are collected just before dawn, and since they are readily digested their importance in the diet is probably under-rated. In only one case were the remains of earthworms visible; all other occurrences were of chaetae, which occurred in 21.4% of adult stomachs and 25.6% of cub stomachs.

Burrows (1968) found a similar but slightly higher percentage occurrence of earthworms in fox scats and stomachs collected from Gloucestershire pastureland. Lever (1959) recorded that earthworms occurred fairly regularly as chaetae but gave no details of percent occurrence. Fairley (1970) did not bother to look for chaetae. The occurrence of earthworms in the diet of foxes was discussed by Jefferies (1974), who showed that the species of worm most likely to occur was Lumbricus terrestris; however it proved impossible to determine the specific identity of the chaetae in the present study. It is interesting to note the regular occurrence of earthworms even in cubs killed in May; it is most unlikely that these were collected by the adults, and the cubs are presumed to be collecting these themselves - in most cases this would only involve a foray of a few feet onto the lawn of the garden in which they are resident. Similarly Murie (1936) thought that cubs collected insects for themselves in late May and June, in his study in Michigan.

The low level of scavenged food items found in the stomach contents is interesting - these formed only 15.6% of the diet in adults and 9.2% of the diet in cubs, and for the cubs the majority of the scavenging occurs in the period immediately after they become independent. This finding is in direct contrast to the many published comments on the subject e.g. Mabey (1973), who wrote that "they seem chiefly interested in rooting about in dustbins". However many of the scavenged food items (sultanas, bread, orange peel, apples, potato peelings, chopped walnuts, lumps of fat, bacon rind, and some of the bones) did not originate from dustbins but were put out for the birds (Royal Society for the Protection of Birds 1971). This is supported by the seasonal occurrence of such items, which are largely confined to the winter diet. Similar scavenged food items have been recorded by many other authors e.g. Lund (1962) found potato peelings in 29/484 fox stomachs from Norway, and Coman (1973) found household scraps consisting of bacon rind, sausage casing, chop bones, bread crusts and cooked meat fragments in 24/967 fox stomachs collected in Victoria, Australia.

Insects never form a major part of the diet in suburban foxes. They occur in 40.2% of the adult stomachs and 41.9% of the cub stomachs, but only constitute 6.4% and 6.0% of the adult and cub diets respectively. Many of the insects were ingested by accident e.g. Fannia maggots were ingested while eating refuse, and the fleas Archaeopsylla erinacei being ingested while feeding on a hedgehog. In most fox food studies the major insect food item was Coleoptera, mainly beetles of the families Carabidae and Scarabaeidae (e.g. Lever 1959).

In London, however, Carabidae were of irregular occurrence and Scarabaeidae were not recorded. Murie (1936) found that in Michigan Scarabaeidae made up almost 100% of the insects eaten. Lepidopteran larvae were the major insect food item in London, 183 specimens occurring in 33 stomachs, these being mostly noctuid larvae. This contrasts markedly with Lever (1959), who only recorded three occurrences of caterpillars (yellow underwing Noctua pronuba from Cornwall and dark arches Apamea monoglypha from Derbyshire and Herefordshire).

Englund (1965a) only recorded two Noctuidae moth larvae in 1166 stomachs from Sweden (and six stomachs containing Agriotidae moth larvae).

As shown in the introduction, most fox food studies show mammals, usually small mammals or lagomorphs, to be the major food item. This is not the case in suburbia. Here wild mammals form 9.3% of the adult and 9.4% of the cub stomach contents, and pet mammals form 2.6% of the adult and 2.1% of the cub stomach contents.

Corke & Harris (1972) have documented the small mammal distribution on the Essex side of London. They showed that the small mammals that extend well into London are *Microtus agrestis*, *Apodemus sylvaticus*, *Sorex araneus* and *Mus musculus*. *Sorex arancus* does not appear frequently in any fox food study, this being attributed to the unpleasant taste of their scent glands (Lever 1959). *Microtus* is the commonest small mammal encountered in suburban fox stomachs, but is still infrequent, this being in contrast to other fox food studies (e.g. Hewson, Kolb & Knox (1975) in Argyll). Foxes were observed on several occasions in London catching these animals on the grassy embankments of railway lines, which provide a regular supply of *Microtus* well into London. Teagle (1964) listed the localities in London at which *Microtus* had been found, Beven (1965) noting that *Microtus* was found within 6 miles of St. Pauls Cathedral. Corke & Harris (1972) also recorded this species on allotments, school fields, and sewage farms. *Apodemus* was of very infrequent occurrence, despite the regular distribution of the species well into London (Corke & Harris (1972)) in gardens, allotments and similar habitats. Most other fox food studies similarly recorded few *Apodemus*; Englund (1965a) attributed this to the agility of the species.

The two occurrences of *Clethrionomys* were in two cubs killed at Hayes (London Borough of Bromley) on the edge of the study area. This species does not extend in beyond the fringes of the suburban area (Corke

& Harris 1972). The infrequent occurrence of Mus is presumed to be due to their tendency to live in buildings, so rendering them relatively immune to predation by suburban foxes. This is in contrast to results obtained in Australia, where Mus musculus is the dominant small mammal in truly wild habitats, and it occurred in 26.3% of 967 fox stomachs, forming 13.7% by volume of the diet (Comon 1973).

The occurrence of Rattus norvegicus and Sciurus carolinensis is not surprising, except that one might have expected a higher level of predation on rats, especially since both rats and foxes find harbourage in the same neglected areas. Rats do not normally feature to any large extent in fox food habits analyses - for instance Lund (1962) only recorded one rat in 447 Norwegian fox stomachs, although Fairley (1970) found a 17% occurrence in adult fox stomachs from north-east Ireland.

The occurrence of only three Erinaceus is also surprising, especially in view of the survey by Morris (1966), who found the hedgehog to be common in London. Studies on den litter suggest that most of these animals are road deaths rather than animals actually caught and killed. The infrequent occurrence of Erinaceus has been recorded by other authors e.g. Lund (1962) found 4 in 447 stomachs, Englund (1965a) found 1 in 1166 stomachs.

Six cases of cannibalism were recorded, four cases by cubs and two cases in adults (both these animals being shot in the same locality). Presumably in the latter case a dead fox was somewhere in the neighbourhood, either having died of mange or being a road casualty. The one occurrence of Meles is presumably due to one of the same causes, since in London this animal is also killed by cars and by Sarcoptes.

The level of predation on domestic pets was remarkably low, and certainly no higher than that recorded in other fox food studies from rural areas. For instance, Lund (1962) recorded 3 cats in 447 stomachs from Norway, and Englund (1965a) found 21 cats in 1166 stomachs from Sweden.

Birds are not normally of major importance in fox food studies. Lund (1962) found 190 occurrences of wild birds in 447 Norwegian fox stomachs (42.5%), and of these only two were of Columba spp. Englund (1965a) found game birds in 20 /1166 Swedish stomachs, and 58 other wild birds in 44 stomachs. These consisted mainly of single Passeriformes. Lever (1959) found birds in 60% of stomachs from lowland areas, and in 40% of stomachs from hill areas, but this figure included all poultry and game birds. In London birds occur in 53.8% of the adult and 79.1% of the cub stomachs. Lever (1959) did not give exact figures, although he stated "thrush, blackbird, starling, chaffinch and skylark were taken more than once", and "wood-pigeons were better represented; probably their bodies would have been found dead by foxes after shooting". Fairley (1970) only found six Columbiformes in 340 adult and 163 cub stomachs in north-east Ireland. In this area Passeriformes occurred in 4% of the adult and 10% of the cub stomachs.

These results are in marked contrast to the present study, where Columbiformes occurred in 10.3% and 11.6% of the adult and cub stomachs, forming 3.8% and 3.7% of the diets respectively. Similarly, Passeriformes occurred in 29.9% of the adult and 65.1% of the cub stomachs, forming 6.2% and 14.9% of the diets. Chickens were not of a more frequent occurrence in suburban fox stomachs than usual - for instance Fairley (1970) found Galliformes in 16% of the adult and 15% of cub stomachs, most of these Galliformes being hens. In the present study comparative figures (for hens only) are 13.7% and 7.0% occurrence, forming 3.5% and 1.8% of the diet. Again predation on domestic birds in London is at a very low level, as was predation on domestic mammals. In total, birds formed 15.5% of the adult diet and 20.5% of the cub diet in suburbia.

This change in food habits of suburban foxes from a high incidence of small mammals to a higher incidence of Columbiformes and Passeriformes is paralleled by the results of Beven (1965) in his study on the food habits of suburban tawny owls (Strix aluco). In rural areas mammals formed a major part of the owl's diet, but in suburban owl pellets there was a marked increase in the occurrence of birds, particularly feral and wood-pigeons, thrushes (especially blackbirds), starlings and house sparrows. With the exception of starlings, exactly the same bird species predominate in the diet of suburban foxes. Yalden & Jones (1970) found similar results for suburban tawny owls in Manchester, but there was no marked predation on Columbiformes.

The occurrence of fruit and vegetables in the diet is in agreement with most other fox food studies, these items contributing a small percentage of the diet. This is in marked contrast to the results of Petrov (1967), who studied Vulpes vulpes karagan in the subtropics of Middle Asia. Here a variety of fruits formed the bulk of the diet.

What is unusual in the suburban fox food studies is the almost universal occurrence of grass in the stomachs (84.6% of adult stomachs and 83.7% of the cub stomachs), often in large quantities, forming 14.0% of the adult stomach contents and 14.0% of the cub stomach contents. Lund (1962) found grass in 247/447 stomachs (55.3%). He suggested that this could be an emetic, and quoted suggestions that in ranched foxes grass is thought to be beneficial for its supply of Vitamin C and in aiding digestion.

7.4.2 Siting of Fox Earths

The data show the importance of raised garden sheds and raised outbuildings for the rearing of cubs in London; in theory any garden shed is a potential earth, although the same sheds seem to be used each year. Stanley (1963) reported that in Kansas occasional fox earths had been reported beneath abandoned buildings, but most dens were 200 or more yards from human habitations. Intolerance of human presence is the norm, and the distribution of fox earths in London (even beneath the front door step in one house) is unusual.

Stanley (1963) studied the factors which affected the distribution of fox earths in Kansas. He found that the type of soil, the presence of water, the presence of cleared areas, and the absence of man were factors which were important in influencing the foxes in selecting their den sites. No such factors were of importance in London.

Stanley (1963) also noted as unusual a concentration of three dens on an island of 53 acres in Kansas River. Similarly Scott (1943) mentioned territoriality in foxes, noting the possibility of intra-specific intolerance during the breeding season. While this may normally be the case, in London litters of cubs can be found very close together - for instance four litters were found in the gardens of one stretch of road, all being situated within a circle of 300 yards diameter. The distribution of relatively quiet gardens seems to be the main criterion in the selection of denning areas.

From the second week of June onwards, the cubs tend to lie up above ground in dense cover, under sheds and in similar cool areas, often being scattered over several adjacent gardens, although they stay in the area of the natal den until the end of September, when dispersal occurs. These observations support the data of Phillips, Andrews, Storm & Bishop (1972). From July onwards the cubs become more independent, feeding themselves to a large extent, and as a result studies on the siting of dens and den litter is only viable up to the middle of June.

7.4.3 Den Litter

As Errington (1935) noted, "in view of the obvious short-comings of the sundry investigational techniques tried for foxes, it seems that the soundest procedure is to rely upon no single technique but use critically all of the methods available", although he also recognized that "stomach analyses are doubtless best for general food habits research".

In the present study den litter in London was studied extensively as an aid to the general food study. Although mammals were in all cases identified to specific level in the stomach contents, it rarely proved possible with bird remains, and in some cases these could not even be identified to the order. Thus what in the stomach is recorded as "Columbiforme" can be identified specifically in the den litter, showing a ratio of Columba livia (including racing pigeons) : C. palumbus of 14.5 : 1. Similarly, Erinaceus in the stomach contents is presumed to be a prey item, yet of the three found outside fox earths two were almost certainly road casualties, and so were scavenged; one was indeterminate.

The den litter is also a valuable study since it confirms the identification of the items in the stomach contents, and also showed that no food items of importance had been omitted in the stomach contents analysis. Only occasional species were found in the den litter which had not been identified in the stomach contents, and none of these were numerically important. Their occurrence is attributed to the larger number of food items found in the den litter.

While den litter is an important aid to study it does present a biased picture of the food habits of cubs during their period of dependence on the adults, as shown in Table 51, where the percentage of the total items in the cub stomachs is compared with the percentage of the total items found in the den litter.

As this table shows, mammals are under-rated in the den litter studies, mainly because small mammals are swallowed whole (none were seen outside earths), and for many larger mammals the bones and fur are ingested as well, and often all that remains is a piece of neatly cleaned back skin. Observations on particular earths showed that mammalian items often disappeared within a day or two. Small Passeriformes are also eaten whole, and hence are under-represented in den litter studies. The reverse is true for larger birds, where the sternum and attached wings persist as play items, accumulating with time, and so becoming over-represented in the den litter. This last point is particularly true for scavenged meat bones, which accumulate around most earths in large numbers but which are relatively unimportant in the

TABLE 51

COMPARISON OF THE RESULTS OBTAINED FROM DEN LITTER STUDIES AND CUB STOMACH CONTENTS ANALYSES FOR THE MONTHS APRIL, MAY AND JUNE. FOR THIS COMPARISON, THE GRASS AND NON-FOOD ITEMS HAVE BEEN EXCLUDED FROM THE STOMACH CONTENTS ANALYSIS, AND THE PLAY ITEMS AND BIRD AND MAMMAL BONES OF UNKNOWN ORIGIN FROM THE DEN LITTER STUDY

	Stomach contents			Den litter	
	Actual % of diet	Number of occurrences	% of total items	Number of occurrences	% of total items
Pet mammals	4.8	6	3.2	13	2.8
Wild mammals	19.6	32	16.9	16	3.4
Chickens	2.0	4	2.1	16	3.4
Columbiformes	7.3	9	4.8	39	8.3
Passeriformes	28.6	47	24.9	68	14.4
Other birds	0	0	0	6	1.3
Unidentified birds	0.2	1	0.5	0	0
Eggs	0	0	0	2	0.4
Scavenged meat, bones, fat	9.3	21	11.1	294	62.4
Other scavenged items	4.8	12	6.4	17	3.6
Insects	10.6	28	14.8	0	0
Earthworms	6.4	11	5.8	0	0
Fruit and vegetables	6.4	18	9.5	0	0
	100.0	189	100.0	471	100.0

diet. Their importance in the den litter is again exaggerated by the fact that several joined bones (e.g. in an extreme case the joined scapula, humerus, radius and ulna of fore-leg of lamb) which were collected as one food item by the adult fox, are pulled apart and scattered by the playing cubs and registered as four food items. Very small food items, particularly earthworms and insects which the cubs collect for themselves, never register in the den litter studies, although such items form a large percent of the food items in the stomach contents; den litter studies are only indicative of the food supplied by the adult.

Similar results were obtained by Errington (1935) in his study of fox food habits in the mid-west of North America.

7.4.4 General Discussion

The food study confirmed the observations of many authors that the fox is an opportunistic scavenger/predator, and will avail itself of whatever food source is available. This is seen in London, where mammals (the staple prey items in rural areas) are rare, and Passeriformes and Columbiformes became of major importance in the diet. Similarly noctuid caterpillars in London replaced carabid and scarabaeid beetles seen in rural studies. Predation on pets and scavenging were of lesser importance in the diet, and are grossly over-rated in popular literature.

SECTION 8
GENERAL DISCUSSION

The term "suburban fox" has been widely used both in popular literature and in the present study. However, no-one has yet decided exactly what is a suburban fox i.e. whether the population of foxes in suburbia is physically isolated from that in the surrounding rural areas, and whether suburban foxes are distinct from rural foxes in behaviour, morphology or in any other aspects of their biology. The aim of this section is to discuss how far the present study has gone in answering these questions, and to decide on the validity of the term "suburban fox".

The "invasion" of foxes into London was documented by Teagle (1967), and these data were discussed in the introduction. It was concluded that at least 35 generations of foxes have been reared in suburban London, and records for individual earths extend back nearly thirty years. The abundance of breeding animals in the study area suggests that the population is self-maintaining, and that it is not dependent upon regular invasions for its continued survival. This assumption was supported by the calculated productivity of the population (Section 5), where it was shown that despite cub control operations at least twice as many juveniles enter the winter population as are needed to replace the adult mortality. It was suggested that the continued invasion of new areas of London is achieved by an excess production of young animals from within the suburban area, and not by continued invasions from the surrounding rural areas.

All the evidence accumulated to date suggests that the suburban fox population is resident and self-maintaining, and as such is physically [and one assumes genetically] relatively isolated from the surrounding rural population[s]. It seems reasonable therefore to consider the foxes in London as a distinct population of 35 years standing, and as such one can examine the effects of urbanisation on the Red fox. Parr (1966) noted that "urbanization and domestication have so much in common that it is very difficult to contrive separate definitions which would be functionally distinct in any fundamental sense". Beck (1973) considered domestication to mean "evolving in a human-protected and human-controlled environment". Since suburban foxes can be considered to have been evolving in a human-protected and human-controlled environment, and since Parr (1966) could not distinguish the process of urbanization from that of domestication it could be said that suburban foxes have been progressively evolving into a state of "domestication" for 35 generations. While only 35 generations of foxes have been raised in such an environment, it is interesting to note that suburban foxes exhibit many behavioural and morphological characteristics which are associated with domestic animals, characteristics which should presumably become more pronounced with time.

While a brief discussion of the significance of the similarities between suburban foxes and domestic animals will be presented, it must be remembered that similar data for rural foxes are slight or absent, and such features as are attributed to being characteristic of suburban foxes might not necessarily be absolutely characteristic of the suburban population only.

The most pronounced of these changes are those of the skeleton, particularly the high incidence of skeletal deformities. This has been discussed briefly in Section 6, where it was shown that a high incidence of pathological conditions of the skeleton has frequently been used to determine whether archaeological material was from wild or from domesticated animals. The incidence of spondylosis deformans, other forms of arthritis, periostitis, osteomyelitis, dental caries and parodontal disease in the skeletal material examined would amply justify the application of the term "domesticated" to suburban foxes, had such material been collected from an archaeological site.

Unfortunately no data are available on the incidence of skeletal pathology in other Red fox populations,but the unusual nature of the present results is indicated by the repeated assertions of Fox (1939) that arthritis was absent in wild canids, and also by the fact that many of the conditions seen in the suburban fox material have not been recorded previously for the Red fox.

Data on variations in the number and condition of the teeth are available for other fox populations. The tooth number in foxes seems to vary geographically (Bree & Sinkeldam 1969) and will not be considered further. Rantanen & Pulliainen (1970) examined the dental conditions of wild Red foxes in northeastern Lapland, and noted that dental caries was absent and that parodontal diseases of a general nature were also absent (although local lesions attributable to accidents were present). This is in marked contrast to the suburban foxes where such conditions are of frequent occurrence.

However, attributing such changes as being directly related to the process of domestication is without foundation. In fact the reason why domestic animals should show such differences from their ancestors has not been explained satisfactorarily. Despite this, however, Drew, Perkins & Daly (1971), in their study of the differences in the micro-structure of bone in wild and domestic animals, claim that differences are evident at the earliest stages of animal husbandry. Berry (1969) came to the conclusion that it is impossible to recognize any traits which inevitably accompany domestication and that most of the criteria by which domestication has been recognized may occur as a result of process which have nothing to do with domestication.

This last point is particularly relevant to suburban foxes, the mode of life of the animals producing morphological changes which, in other animals, have been attributed to the process of domestication. Thus pathological conditions in the skeleton are accentuated by trauma. Wells (1964) noted that when the overall stress of life eases for a particular human race they tend to be less afflicted with osteoarthritis. As an example of one form of stress, it was shown in Section 6 that the physical trauma incurred as a result of car injuries accentuated the development of spondylosis deformans. The high incidence of broken bones in suburban foxes, mainly due to car injuries, is unlikely to be seen in many other fox populations, since these will not come into such regular contact with motor vehicles. As a result, if spondylosis is present in other fox populations it is unlikely to be so well pronounced.

A similar situation is seen in deer populations. Cowan (1946), sampling from the remote parts of British Columbia, found very few cases of pathological conditions in the skeleton of Columbian Black-tailed deer (Odocoileus hemionus columbianus). The two cases of arthritis he described were "selected from among several thousand normal deer". In contrast, Chapman & Chapman (1969) studied road-killed Fallow deer (Dama dama) from Epping Forest, this population being subject to heavy "predation" by motor vehicles. They noted that many deer showed evidence (from fractured bones) of having been involved in accidents prior to the fatal one, and often associated with this were degenerative lesions of unknown aetiology.

Similarly, nutritional stress is important in the development of pathological conditions in the skeleton. Glenney (1956) noted the earlier occurrence of spondylosis deformans in dogs subject to Vitamin A deficiency, and Wells (1964) noted that in man the amount of arthritis declines with an improvement in the nutritional status.

Whether suburban foxes are suffering from a deficiency of certain vitamins is difficult to determine since the daily vitamin requirements of the fox are not known, neither has the vitamin intake been determined in the present food study. However, during part of the year the paucity of vertebrate prey items in the diet, and the frequent occurrence of scavenged food items, suggests that some vitamin deficiencies may occur.

This assumption is supported by the frequent occurrence of sarcoptic mange in suburban foxes (30% of the winter-killed animals were suffering from this disease). This form of mange is found almost exclusively in animals killed in suburban habitats, and animals killed in the surrounding countryside are remarkably free of the disease. Several factors contribute to this state of affairs, and again the nutritional state of the animal is important.

Anon. (1971) noted that "mange develops best if the host is predisposed to it by factors like vitamin A deficiency, protein deficiency .... ", vitamin A deficiency also being attributed as a cause of the skeletal deformities (Glenney 1956).

The high population density of suburban foxes also assists the development and rapid spread of mange, as does the behaviour of the animals. In London a variety of discontinuous habitats exist, and only a few habitats are suitable as a daytime refuge (overgrown gardens, railway cuttings, old buildings and factory yards being those most frequented), since areas subject to regular disturbance by people or dogs are avoided. As a result, foxes aggregate to lie up during the day, several adult foxes occurring together in one small area. An extreme example was of four adult dog foxes being removed from under one garage floor during the winter months (a fifth fox of unknown sex was lost). Such contact promotes the spread of the disease. Random observations suggest that in London defended territories as postulated by e.g. Burrows (1968) do not exist, there being a greater degree of contact between suburban foxes, this presumably resulting in a greater degree of stress, and stress also renders the animal more susceptible to mange. More detailed work on mange is now in progress, and so no data have been presented in this thesis.

The results of the food study were not surprising in revealing that suburban foxes ate whatever was available to them, the adaptability of the fox in its food habits being widely recognised as one of the major factors contributing to its success. It was of interest to see that both suburban foxes and suburban tawny owls, which normally feed mainly on mammalian prey, readily adapt to taking avian prey, despite the infrequent occurrence of such food items in rural areas.

The age structure of the suburban fox population is remarkably similar to that determined for most other fox populations studied, despite the very different habitats from which the populations were sampled. In the different populations examined the only statistically significant differences seen were in the ratio of young : adults, this ratio reflecting the intensity of control operations. The relatively light control to which suburban foxes are subjected does not affect adult survival or longevity.

Thus in conclusion it can be seen that the term "suburban fox" is valid, and that suburban foxes form a distinct, self-maintaining and expanding population. These animals inhabit a unique environment that imposes various stresses on the population, such stresses being exhibited in the various diseases which appear to be prevalent in suburban foxes but are rare elsewhere.

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Syndactyly in the Red fox, *Vulpes vulpes*

Introduction

Syndactyly occurs naturally in some groups of birds, e.g. Coraciiforms such as kingfishers in which toes III and IV are closely joined and mammals, e.g. Perameloidae and Phalangeroidea in which the second and third toes of the hind feet are united by a web of skin. Syndactyly as a pathological condition has been reported in a number of mammalian families and can exist in any degree from cutaneous webbing to synostosis of bony elements. Since reference to this condition is widely scattered in the literature, a brief review of the incidence of syndactyly in mammals is given.

Lyne (1953) reported syndactyly of both mani, with digits III and IV conjoined, in the pouch embryo of the wallaby *Thylogale billardierii.* In man, syndactyly occurs either as an isolated finding or as a feature of certain malformation syndromes. Rubin (1967) described this as one of the commonest hand deformities, although he also stated that syndactyly is more frequent in the foot than the hand; however Eldridge, Smith & McLeod (1951) stated the reverse to be the case in man, as in swine and cattle. Bateson (1894) noted that in the human hand there is a considerable preponderance of cases of union between digits III and IV, whereas if two digits in the foot are united they are nearly always II and III.

In rodents Frank (1959) described a recessive mutant in laboratory *Microtus arvalis* where two digits, commonly III and IV, are joined by a common epidermal sheath. This occurs more commonly in the hind feet and represents the minimal type of digital attachment. Grüneberg (1963) considered this condition to be a special case and referred to it as "epidermal syndactyly" since in all cases of "primary" syndactyly digits with soft-tissue fusion are joined by skin complete with all its layers. Grüneberg (1956, 1960, 1961, 1962, 1963) has described three forms of syndactyly in the laboratory mouse, synostosis occurring in all three types. These three mutants are syndactylism (*sm*/*sm*), oligosyndactylism (*Os*/+) and shaker with syndactylism (*sy*/*sy*). Center (1966) described another case of syndactyly in this species, the *jt* form, where only the skin and subjacent soft tisue, usually of digits II, III and IV, are affected in a proximo-distal direction. Johnson (1969) described a polysyndactylous gene which arose in the laboratory mouse during a neutron irradiation experiment.

Most instances of syndactyly are from the artiodactyls and it was once thought that this was simply an exaggeration of the normal fusion of metacarpals and matatarsals III and IV, which form the cannon bone, to include the phalanges. However Grüneberg & Huston (1965) have shown that developmentally this is not the case. In swine, syndactyly has occurred in several breeds in Europe, whereas in North America there are few recent records (Leipold & Dennis, 1972). Bateson (1894) noted that syndactyly in the pig commonly affects fore and hind feet simultaneously. Dennis & Leipold (1972) noted that dactylous conditions occur only rarely in sheep, but when syndactyly does occur the hind feet are involved to a greater degree than the fore feet. In the Cervidae, Lönnberg (1930) recorded a specimen of *Odocoileus peruvianus consul* with digits III and IV of both fore feet affected. In cattle Leipold, Adrian *et al.* (1969) reported that syndactyly has recently been noted in four breeds: Austrian Spotted Mountain, Indian Hariana, Japanese Improved and U.S. Holstein-Friesians. In the latter breed its incidence, inheritance and anatomy have been extensively studied. This type of syndactyly is a recessive hereditary

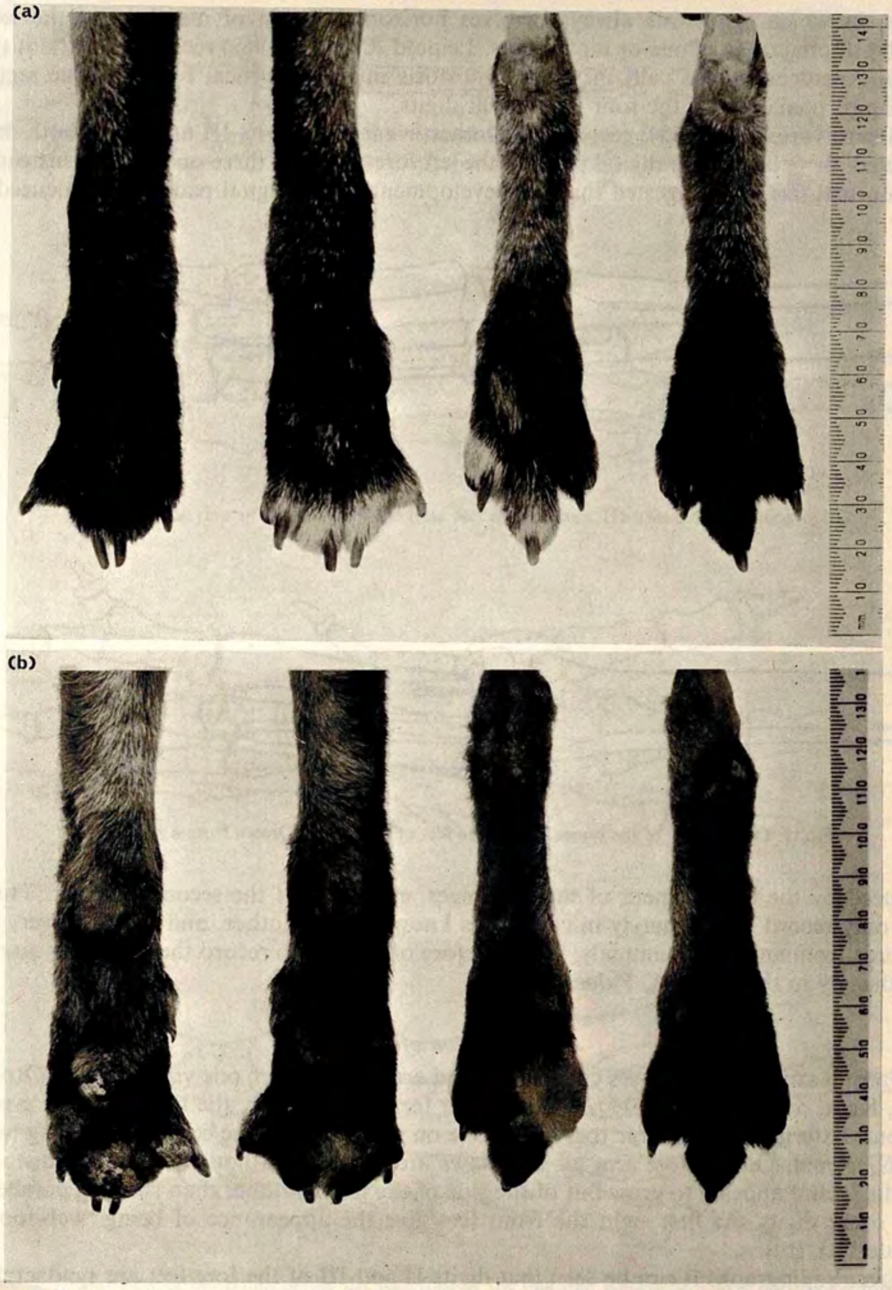

PLATE I. External views (a) dorsal and (b) plantar of the vixen's feet, displayed in the order left fore, right fore, left hind and right hind.

form, in which synostosis always involves horizontal fusion of members of the same pair(s) of phalanges of one or more digits. Leipold & Guffy (1969) recorded a variant type in an Aberdeen Angus calf, in which synostosis involved vertical fusion of the second and third phalanges of the four main front digits.

In carnivores Abe (1954) recorded a Domestic cat with digits III and IV of both mani affected, there being four digital pads on the left fore-paw and three on the right instead of the normal five. He suggested that the development of the digital pads was influenced or induced by the development of the phalanges, especially of the second phalanx. This is the only record of syndactyly in carnivores known to the author, and there are very few records from any wild mammals. It is therefore of interest to record the following cases of syndactyly in the Red fox, *Vulpes vulpes.*

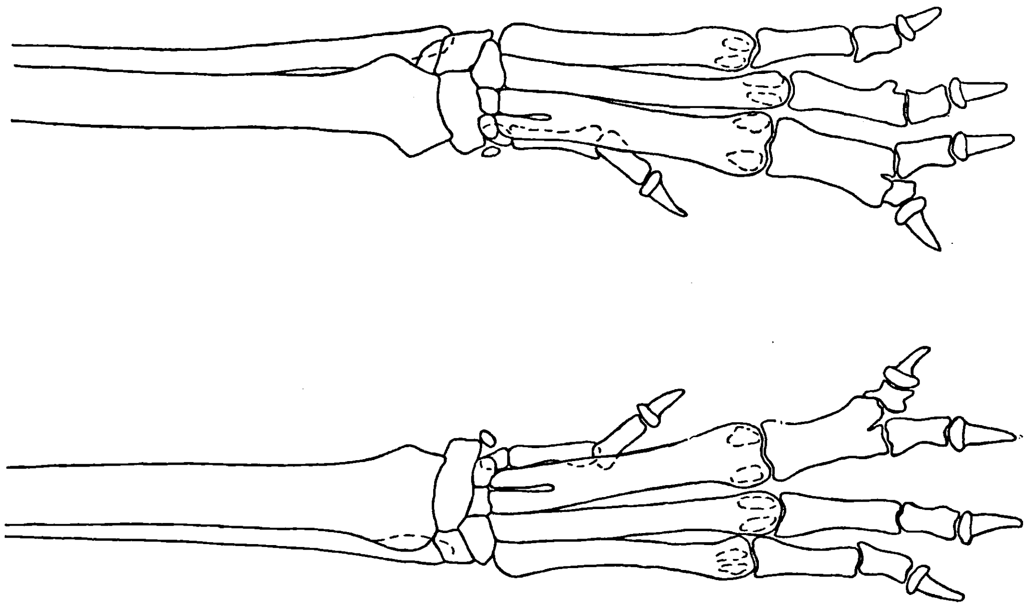

FIG. 1. Dorsal view of the bones of the fore feet of the vixen. (Drawn from a radiograph).

Description of cases

From a sample of 350 foxes collected in and around London, one vixen, shot in Orpington, Kent, on 24th August 1972, had all four feet syndactylous, the hind feet to a greater extent. Externally, only three toes are visible on the hind feet, the central one being wider than normal. On the fore feet all five claws are separate, although digit II is distorted medially and appears to grow out of the side of the manus rather than running parallel to the other digits. At first sight the front feet give the appearance of being 'web-footed' (Plate I(a), (b)).

From radiographs it can be seen that digits II and III of the fore feet are syndactylous for most of their length (Fig. 1). The metacarpals of these digits in both mani are separated

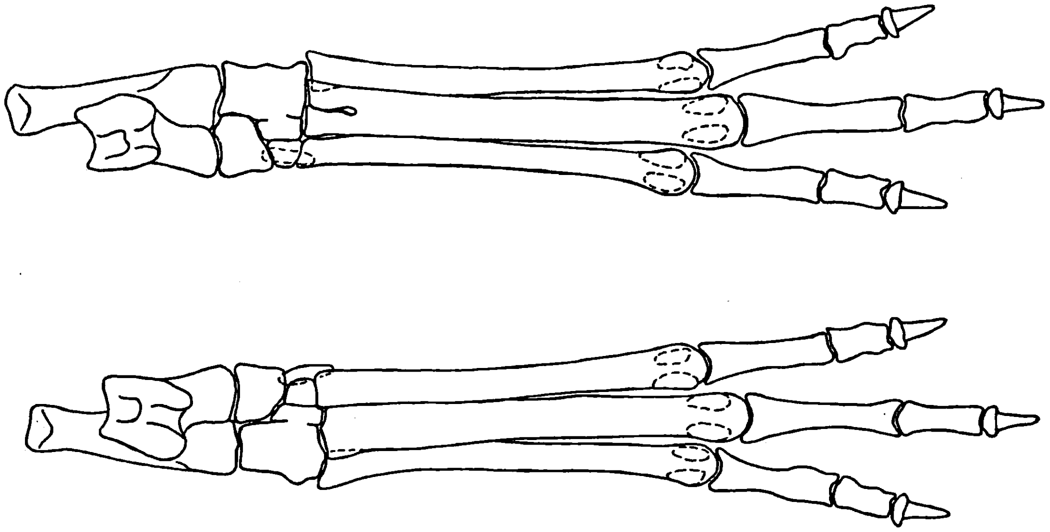

FIG. 2. Dorsal view of the bones of the hind feet of the vixen. (Drawn from a radiograph).

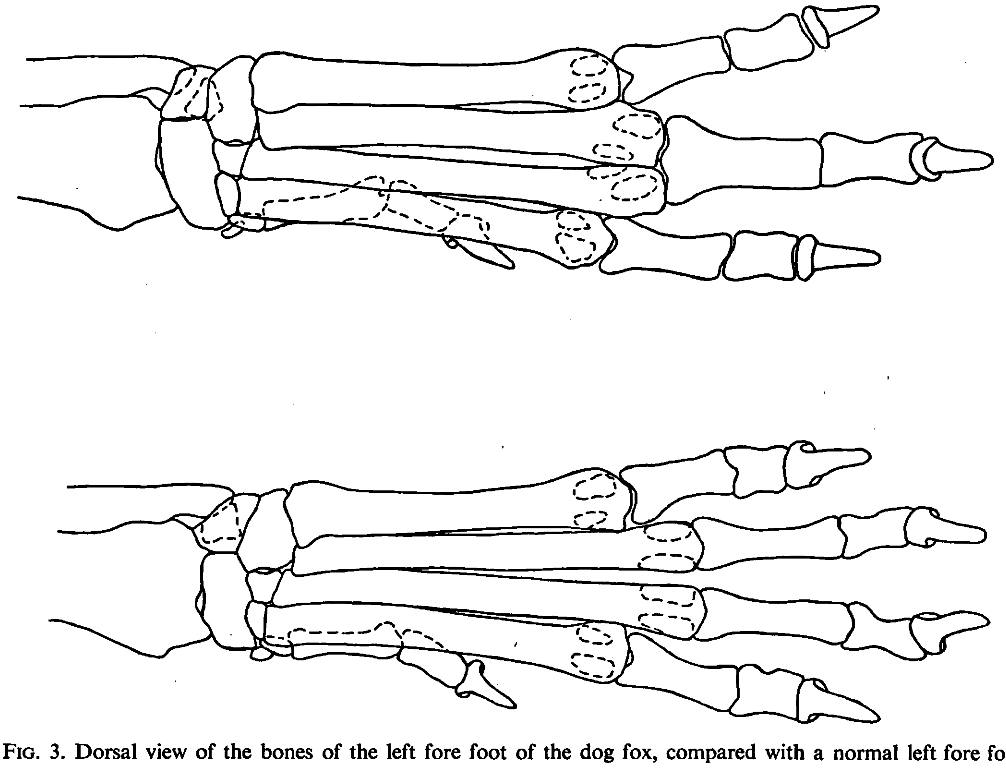

FIG. 3. Dorsal view of the bones of the left fore foot of the dog fox, compared with a normal left fore foot below. (Drawn from a radiograph).

but closely applied at their proximal ends. For the rest of their length the metacarpals are fused, although two articular surfaces are present at the distal end of the fused metacarpals. Only two sesamoids are present at the distal end of the fused bones. The first phalanges of these digits are fused proximally but still retain two separate concavities that articulate with the metacarpals. These fused bones diverge at their distal end, the first phalanx of digit II forming an acute angle with that of digit III. Phalanges 2 and 3 are separate. The carpal bones are unaffected.

In the hind feet, toes III and IV are completely fused throughout their length (Fig. 2). In the left hind foot the two metatarsals are distinct proximally, although in the right hind foot the metatarsals are fused throughout. Only two sesamoids are present on the fused metatarsals, and all three phalanges are completely fused. Tarsal bones III and IV are fused laterally.

From a sample of over 1600 foxes collected from Kent, Surrey and Wales syndactyly was noted in only one animal, a dog fox, shot in Coopers Wood, Kent, on 10th March 1966 (H. G. Lloyd, *pers. comm.*). In this animal the fore feet only are affected. Externally, only three toes are visible, the central toe being markedly wider than those on either side.

From radiographs (Fig. 3) it can be seen that digits III and IV are involved. The two metacarpals remain separate, although they converge distally and come to lie close together. This contrasts with the normal manus wherein the metacarpals diverge. The adjacent sesamoids of the affected digits are reduced and displaced proximally. Synostosis involves the phalanges alone, all three being fused throughout their length. The first phalanx is much wider at its proximal end and here has two separate concavities that articulate with the two metacarpals.

Discussion

Woodhead (1969) published a photograph of the feet of a vixen shot in the North of England in which only three toes were visible externally on all four feet. The hind feet are identical in appearance with the vixen described here but the toes of the fore feet appear to have reached a greater degree of fusion. It seems probable that in both animals the same underlying genetic cause was involved, a variable manifestation of syndactyly having been noted by a number of authors (Grüneberg & Huston, 1965; Leipold, Adrian *et al.*, 1969).

Eldridge, Smith & McLeod (1951) reported that syndactylous Holstein-Friesian cattle are "unthrifty", less agile and have a marked tendency for the feet to become sore. Similarly Leipold & Dennis (1972) noted a syndactylous pig as being "runty" and in poor condition. However, neither of the affected foxes appeared to be adversely affected in any way as a result of syndactyly (although the vixen from Orpington was badly infected with *Sarcoptes scabiei*, which currently commonly infects foxes in that area).

Bateson (1894), when discussing syndactyly in ungulates, noted that "as . . . in Man . . . if the union is incomplete, as it commonly is, the peripheral parts are the least divided, the division becoming more marked as the proximal parts are approached". This is certainly the case in the dog fox described here, but the reverse holds true in the vixen, in which synostosis in the fore feet is least pronounced distally. It is apparent that the two cases of syndactyly reported here are of different genetic origin. It is of interest to note the absence of records of syndactyly in wild mammals, especially carnivores, in view of the fact that three instances in the Red fox have recently been observed.

My thanks are due to Mr N. Vessey of the London Borough of Bromley who supplied the vixen and Mr H. G. Lloyd for the loan of the other specimen. I would also like to thank Messrs M. Colthorpe and S. Horrell for their assistance with the photography and Dr G. I. Twigg for critically reviewing the manucript. This work was carried out while in receipt of a postgraduate research grant from the National Environment Research Council.

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