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Age determination in the Red fox (*Vulpes vulpes*)—an evaluation of technique efficiency as applied to a sample of suburban foxes

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(With 2 plates and 5 figures in the text)

A review of age determination techniques that have been applied to the family Canidae is presented. It is shown that the pattern of growth and development of the various species is very similar, the rate of development being greater in the smaller, shorter-lived species, and *vice versa*.

The occurrence of annuli in the hard tissues of London foxes is demonstrated; these annuli can be used reliably for age determination, despite suggestions that temperate zone animals from weakly continental climates have indistinct annuli. The objective ages determined by cementum annuli are then used to investigate the value of less time-consuming age determination techniques, particularly in the separation of the young-of-the-year from adults. The results obtained from different studies vary, and these differences are discussed. It is suggested that the speed of development varies slightly in different Red fox populations, and so caution must be exercised before data from one population are applied to another population.

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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) showed that age data are particularly valuable in the management of a game species, and Spinage (1973) 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. Broad age groupings may suffice for studies of productivity, social behaviour, etc. but for studies on population dynamics different generations need to be recognizable. 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, age structure and longevity, the numerically larger generations having a shorter life span, and the numerically small generations having raised indices of life span and fertility.

Although desirable, the determination of an animal's exact age often raises difficulties. Thus Taber (1971) 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 the criteria of age are generally somewhat less precise for mammals than they are for birds and, since these processes of growth are to some extent controlled by health and nutrition, they may be slower in one individual and more rapid in another.

An investigation into technique efficiency was a necessary prerequisite to a more detailed investigation into the age structure of London's fox population (Harris, 1977). A study of age determination techniques for the Red fox is slightly simplified since the species only has one litter a year, and so any technique that can separate year classes clearly also separates generations. Most fox cubs in London are born at the end of March, with one month's variation either way, so that theoretically one can determine the animal's age ± one month. Two techniques are desirable in a study of Red fox population dynamics:

(1) A quick simple technique that can separate animals less than a year old (hereafter called juveniles) from adults (one year and over). This technique may be subjective or objective, and is particularly valuable since Harris (1977) has shown that the juvenile age class is numerically dominant (50–80% of a winter sample) and ecologically the most important.

(2) An objective technique to determine the exact age of adult animals. Such a technique may be time consuming, but only need be applied to a small proportion of the sample when used in conjunction with the first technique.

Several possible methods of age determination have been examined previously in the Red fox, but only limited attempts have been made to correlate the results obtained from these different methods when applying them to the same individuals. Moreover, many of the results are contradictory, with different conclusions being drawn from studies on different populations, so that it proved necessary to rationalize these results before utilizing them in a population study, and particularly to decide which techniques, if any, fulfilled the two requirements above.

No detailed literature review will be included since several such reviews have been published already (Taber, 1971; Morris, 1972; Spinage, 1973). Reference will be made, however, to relevant literature on age determination in canids. The material used in the present study consisted of 336 animals (168 of each sex) collected in London between November 1971 and November 1973. The age distribution of the sample is given in Harris (1977). It must be noted that owing to the varying condition of the specimens each technique was not necessarily applied to every animal.

Incremental lines of the dentine, cement, and the periosteal bone of the lower jaw

Introduction

Annuli have been used extensively in mammalian age determination, and the technique has been reviewed in detail by Klevezal' & Kleinenberg (1967). Both cement and dentine are laid down appositionally, dentine on the internal surfaces of the tooth and cement externally around the root. As a result, growth of the dentine is limited by space and is a relatively transient process, ceasing in most mammals soon after maturity is attained, and so in most mammals the study of cement sections is more valuable than that of dentine sections. This applies also to carnivores, despite the fact that in this group the cement layer is far thinner than in herbivores.

Annuli have been demonstrated in the hard tissues of relatively few wild canids. Linhart & Knowlton (1967) studied the coyote (*Canis latrans*); using 30 known-age skulls and the teeth from 156 animals of unknown age they found that the first opaque layer was formed in the cement of the canine at 20–23 months of age, and that accurate counts could be obtained up to 21 years of age. Similarly, Lombaard (1971) found that in the Black-backed jackal (*Canis mesomelas*) the annuli were best developed in the canine teeth, with the first opaque band being formed at about 10 months.

Smirnov (1960), quoted in Klevezal' & Kleinenberg (1967), noted the presence of layering in the cement of *Vulpes vulpes*, *Alopex lagopus* and the wolf (*Canis lupus*), but commented that such layering did not occur in all specimens. In the same review, however, Klevezal' & Kleinenberg (1967) described their own work on captive *Alopex lagopus*, in which they demonstrated annual layers in the dentine, cement, and in the periosteum of the lower jaw. They found that in the dentine many accessory bands made it difficult to determine the annual layers, the tooth cementum lines being more distinct. The periosteal layers of the mandible were best developed in the region of the last premolar or first molar. To date this is still the only wild canid in which annuli have been demonstrated in the periosteum. Grue & Jensen (1976) have described annuli in the cementum of Arctic foxes from Greenland and Denmark, and discussed factors affecting their clarity.

In the Red fox, Jensen & Nielsen (1968) demonstrated the use of cementum lines of the lower canines to determine the age of Danish foxes, and Johnston & Beauregard (1969) used a similar technique in a study of rabies epidemiology in Ontario. Grue & Jensen (1973) supplied further data on the formation of annuli in the cement of *Vulpes*, using 135 known-age wild foxes with an age range of five months to four years. They found a complete correspondence between the number of annuli and the known-age in foxes less than a 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 the darkly staining line became distinct at any time from March through to the autumn.

Monson, Stone & Parks (1973) investigated the use of annuli in determining the age of 50 captive and 15 wild Red foxes in New York State. Sagittal sections of the 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, the accuracy of age determination was 45·7%, whereas using the premolars an accuracy of 90% was obtained, when combining the estimates of three observers. These authors concluded that sections of the 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. In contrast to Grue & Jensen (1973) and Monson *et al.* (1973) he found a 100% agreement between the known ages and the ages estimated by cementum annuli. Bree, Soest & Stroman (1974) aged their Red fox material by counting lines in the dentine, these being demonstrated by cutting the canine in half, polishing and etching the cut surface and then staining it with toluidin blue. They did not, however, attempt to show the clarity of these lines, nor the reliability of the technique, and as other authors have found dentine lines to be unreliable for age determination the technique requires further investigation before being used in population studies.

Preparation of tooth and jaw sections

The left mandible was cut transversely into short sections, each section holding one tooth. In the early specimens the complete jaw was used, but in later specimens only the canine and premolar sections were used. The sections were decalcified in a 3% solution of nitric acid in 10% formaldehyde (Drury & Wallington, 1967). Once the bone began to feel soft complete decalcification was determined using the technique of Mahoney (1966). When all the calcium salts had been removed the tissue was neutralized in a 5% solution of sodium sulphate for 12 hours and stored in 70% alcohol prior to sectioning.

During sectioning the teeth were left in the mandible and sections were cut on a freezing microtome, these having a thickness of 10–30 μm. Sagittal sections of the premolar and molar teeth were cut, thereby also giving a transverse section of the mandible. For the canine, both longitudinal and transverse sections were cut. The sections were stained in Delafields Haematoxylin and mounted in Glycerine Jelly.

Results and discussion

In the periosteum many lines were visible, their number increasing in sections taken further back along the lower jaw. The number of lines showed no correlation with age, sections taken from the same region of the lower jaw in animals of very different ages showing the same number of lines, and animals only a few months old exhibiting several lines. This pattern of deposition was far less regular than that recorded in Ontario by Johnston & Beauregard (1969), who found that two lines per annum were laid down in some parts of the bone, while only one per annum was laid down in other areas.

The pulp cavity of the teeth is closed progressively during the second year of life, when the first annulus is deposited in the secondary dentine, and by the end of the second year the cavity is reduced to a narrow canal. Thereafter, deposition of the secondary dentine is progressively reduced each year, with the result that the annuli become less distinct.

Counting such lines is difficult in older animals and was found to be unreliable in animals four years of age and older. This decrease in the size of the pulp cavity is, however, invaluable for separating animals in their second summer and autumn from older animals, since the difference in the size of the pulp cavity can be demonstrated 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 due to a pathological condition in which the teeth were reduced to hollow shells. A similar sequence of events was recorded in *Alopex lagopus* by Dolgov & Rossolimo (1966), who used the size of the pulp cavity to divide a winter sample into juveniles, animals 1–2 years old, and older animals.

Only sections of the tooth cementum gave growth lines which could be demonstrated consistently (Plates I and II) and which could be matched with the age of the animal as roughly estimated by other techniques. In the molars and incisors the growth lines were difficult to demonstrate and usually so closely packed that accurate counting was difficult. Longitudinal sections of the canines were difficult to interpret near the root, where the annuli are often split and distorted (Plate I(b)), although along the length of the canine an accurate count could often be obtained, despite the close spacing of the lines. These annuli were counted more easily on transverse sections of the canine root (Plate I(c)), the annuli extending along the length of the root to the gum line, although they become progressively crowded as they reach the gum line.

The most easily interpreted tooth sections were sagittal sections of the premolar teeth, so long as care was taken to ensure that (a) the section was vertical and (b) that it passed through the centre of root. In the premolars the annuli are clear, uniformly spaced, even in old animals (Plate I(a)), and only rarely split into the subsidiary lines which make interpretation of canine sections more difficult and less reliable.

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. In some animals the new annulus was only visible in one or two teeth, and presumably would later become distinct in all teeth. No set pattern was detected, the annulus in some animals appearing first in the molars or last premolar, whilst in other animals it was detected first in the canine.

For an accurate assessment of an animal's age it is important to section more than one tooth because different teeth from the same animal may yield slightly different counts (Table I), and so the determined age should be based on sections of at least two teeth.

Since it has been shown by earlier workers that skill in interpretation of slides is the main source of error in age determination, a check was made on the ease and accuracy of interpretation, using a sample of 237 canine and premolar sections from 76 animals. With an experienced and an inexperienced worker there was 84% agreement in the interpretation of individual slides (Table II), and by using sections of two or more teeth per animal there was 88·1% agreement in the determination of the age of individual animals. It is probable that after a period of practice by both recorders a greater degree of agreement would be obtained, since the level of disagreement in the interpretation of individual slides decreased progressively during the trial period. As this trial sample included mostly summer-killed animals, when interpretation of sections is more difficult, a greater degree of correlation would be expected in a sample of winter-killed animals, which formed the bulk of the material used in this study.

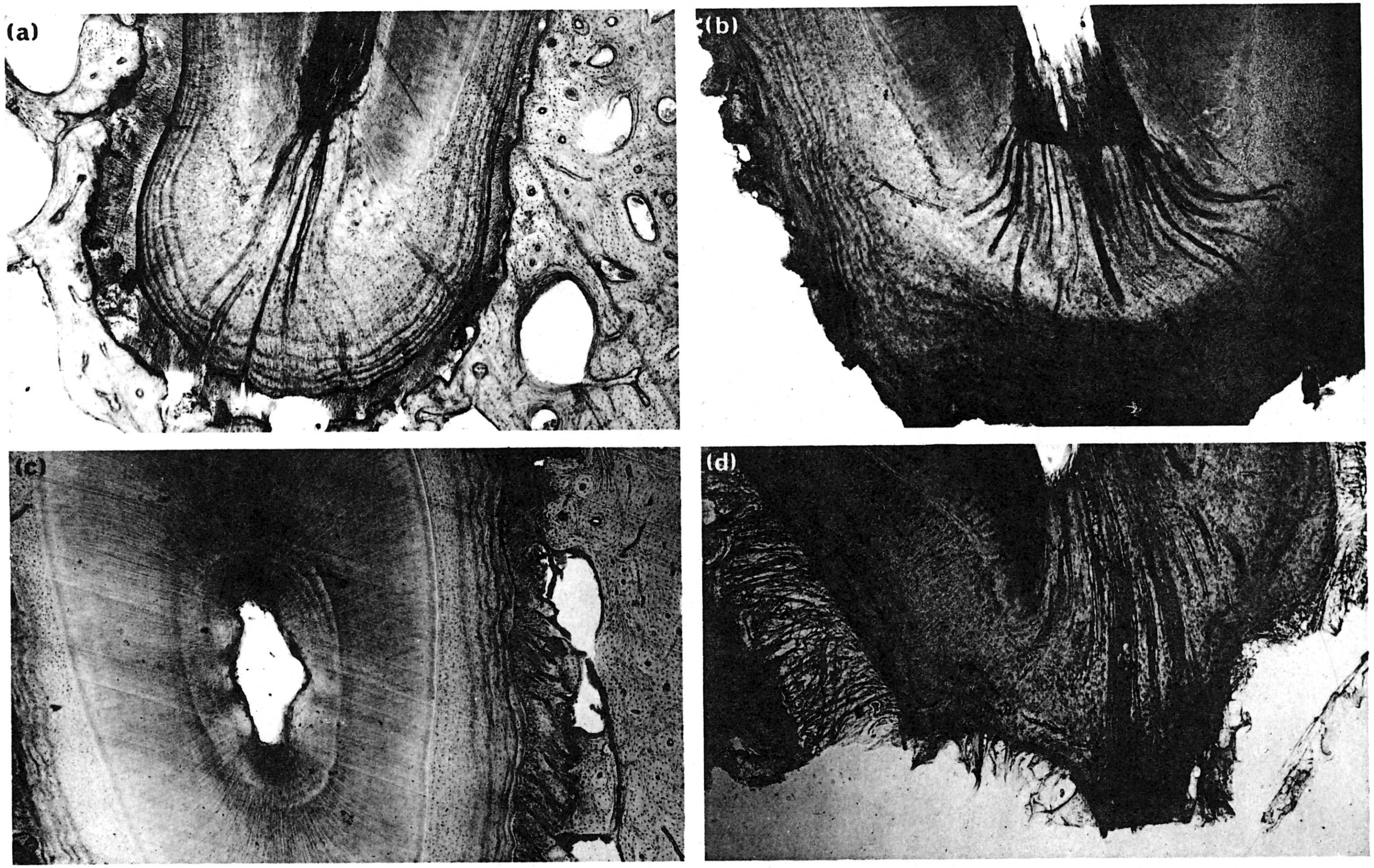

PLATE I. Annuli in the cementum of fox teeth. (a) Sagittal section of P_2 of an animal killed in late October, showing five evenly spaced annuli, the sixth annulus only just becoming distinct. (b) Longitudinal section of the canine of the same animal, showing the difficulty in interpretation of such sections in old animals. The annuli are indistinct on the sides of the root, and divided into many subsiduary lines at the tip. (c) Transverse section of the canine root of an animal killed in September. Five distinct annuli can be seen in the cementum, less distinct annuli in the secondary dentine. (d) Longitudinal section of the canine root of an animal killed in May. Two distinct annuli are visible on the sides of the root, the third annulus just becoming distinct.

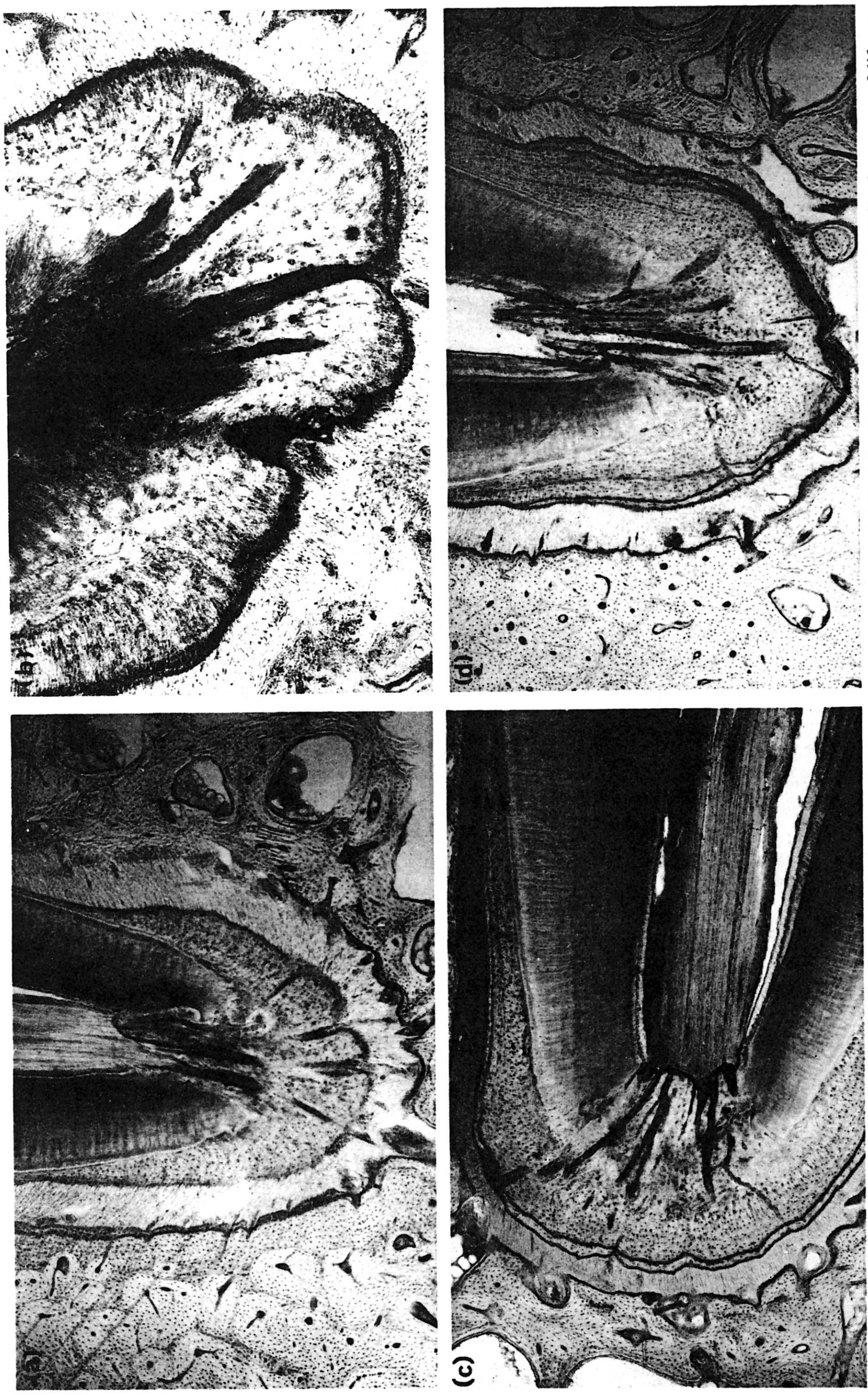

Plate II. Development of annuli in sagittal sections of the premolar teeth. (a) P_3 of an animal killed in February at the end of its first year of life; no annulus has yet been formed. (b) Tip of the root of P_3 of an animal killed at the end of April, with the first annulus just becoming distinct. (c) P_2 of an animal killed in February at the end of its second winter; one clear annulus is present in the cementum, extending to the gum line. A clear annulus is also present in the secondary dentine. (d) P_3 of an animal killed in March at the end of its third winter, two clear annuli being visible in the cementum. Less distinct annuli are present in the secondary dentine.

TABLE I

Comparison of annual growth line counts in animals with four different teeth (canine to fourth premolar) sectioned

	Number of animals	%
All sections agree with assessed age	129	82·8
One section disagrees with assessed age	23	14·6
Two sections disagree with assessed age	5	3·2
Total	157	100·0

Jensen & Nielsen (1968), Grue & Jensen (1973), Monson *et al.* (1973) and Allen (1974) have all demonstrated the accuracy of cementum annuli in age determination in the Red fox, showing that skill in interpretation is the main source of error. The present sample came from an area with a very mild winter climate (Chandler, 1965) and so may not be expected to exhibit clear annuli since Klevezal' (1973) has noted that animals from areas with a weak continental climate have poorly developed annual layers, and that counting these layers is more complicated than with animals from regions with a marked continental climate. However, no difficulty in slide interpretation was found, a high degree of correlation being recorded by two observers, and consequently the technique was used to determine the objective age of the sample. This standard was then used to determine the value of other, less time-consuming techniques in the estimation of age, particularly in separating juveniles from adult animals.

TABLE II

Comparison of section interpretation by an experienced and inexperienced recorder, using 237 sections from 76 mainly summer-killed animals

	Number of sections	%
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

Use of the baculum in age determination

Introduction

Many authors have shown that the general pattern of growth of the baculum is for a rapid increase in length in juvenile animals, this slowing at the onset of puberty, and for the bone to become thicker and heavier under the influence of sex hormones. Hildebrand (1954) described the morphology of the mature baculum of several canids.

In canids the baculum is of limited use for purposes of age determination. Dolgov & Rossolimo (1966) showed that in *Alopex lagopus* there was a great variation in the form and size of the baculum. Using a weight to length ratio they showed that animals up to a year old were distinct from animals of the previous year when comparing animals sampled at the same time of the year, but thereafter the samples were mixed. Lombaard (1971) found that in *Canis mesomelas* immature and mature bacula looked alike, and that no change in shape could be observed from the age of two weeks to five years. He found that monthly samples showed considerable overlap in length and weight measurements, although he could separate animals less than five months old (immature) from older (mature) animals. The maximum weight and length of the baculum was achieved rapidly between the fifth and sixth months.

Bree, Chanudet & Saint Girons (1966) studied 126 Red 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 g 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, and they modified their views, reporting that foxes with a baculum longer than 45 mm and heavier than 400 mg were sexually mature. They made no attempt to present data showing the degree of separation of juvenile animals 6–9 months old from adults, this being the important age at which the juveniles enter the adult population, although it would appear from their graph that there was considerable overlap between the baculum size of juvenile and adult animals.

Methods

The bacula were cleaned by removing the bulk of the flesh manually and then gently boiling the bone in a 2·5% solution of sodium perborate to remove any remaining meat and to bleach the bone (Chapman & Chapman, 1969). Any remaining fat was removed by soaking the bone in acetone. The bacula were then measured with a pair of callipers to the nearest 0·1 mm and weighed to the nearest mg; any exhibiting old injuries were discarded.

Results and discussion

The Red fox baculum is similar to that of most other canids (Fig. 1). 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 $\frac{2}{3}$ to $\frac{4}{5}$ of the length of the bone, causing it to be V-shaped in cross-section. The apex is bent ventrally through an angle of 10° to 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 apex is flattened or oval in shape and often bifurcated; in *Alopex* the bifurcation deepened with age, while in *Vulpes* the reverse trend was apparent 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 change could not be quantified. The young baculum exhibits the same general shape as that of the adult, but is made of porous bone and is often fenestrated. During growth there is no change in shape, and these fenestrae may persist in some young adults.

From Fig. 2 it can be seen that the baculum undergoes a period of rapid growth in length until a length of 40 mm and a weight of 200 mg is reached, this occurring 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 (Fig. 3), and concomittantly the baculum begins

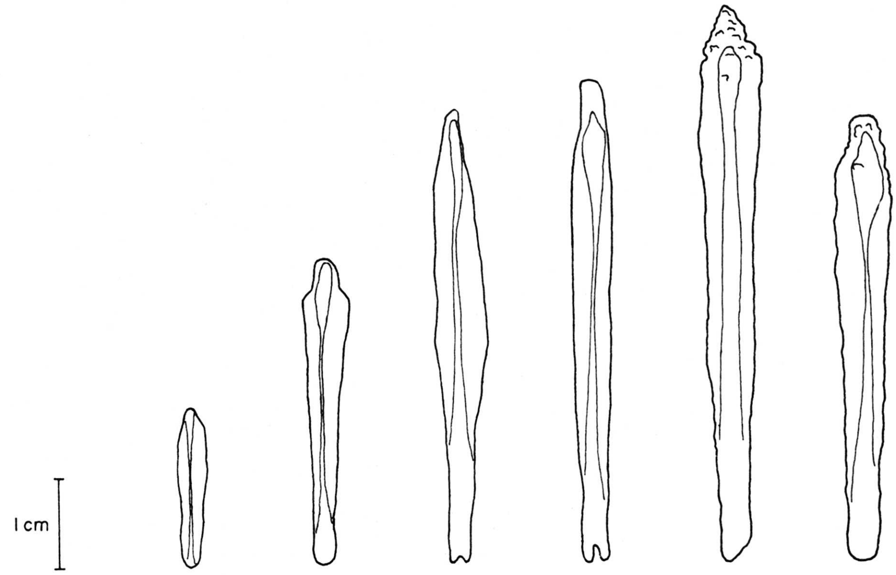

FIG. 1. Changes in the morphology of the baculum with age. All are dorsal views with the apex of the bone facing downwards. From left to right the ages of the animals were six weeks, fourteen weeks, seven months, eleven months, eight years, seven years.

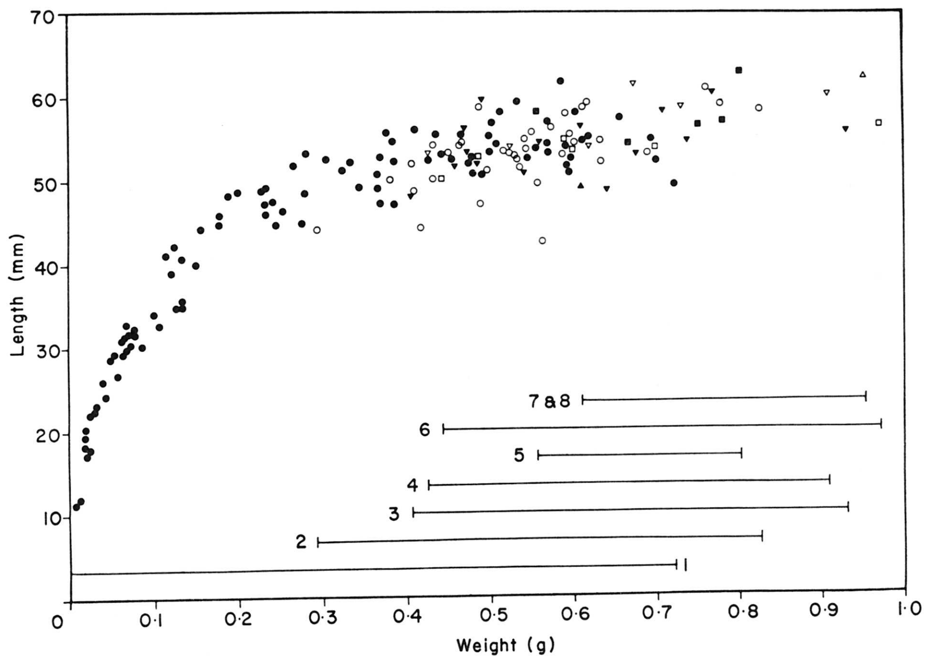

FIG. 2. Growth of the baculum with age. Symbols denote: ● first, ○ second, ▼ third, ▽ fourth, ■ fifth, □ sixth, ▲ seventh, △ eighth year class. The horizontal lines mark the range of weights recorded for each year class.

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 weight is obviously the more useful measurement but, as Fig. 2 shows, any animal with a baculum weight in excess of 275 mg (and a length in excess of 42·5 mm) may be either first or second year animals, and those with a baculum weight in excess of 400 mg (and a length in excess of 45·0 mm) may belong to any of the eight year classes. When comparing the baculum weights of monthly samples, 100% separation of juvenile and adult animals can be achieved only to the end of September, when the juveniles are only six months old. In the sample October to December, juvenile bacula weighed up to 600 mg. When examining all the bacula of 600 mg or less in weight, 20/25 (80%) were juveniles, four (16%) second-year animals and one (4%) was a third-year plus animal. In the January to March sample juvenile bacula weighed up to 750 mg and showed a complete overlap in the range of weights with older animals; of the 57 animals with a baculum weight of less than 750 mg 31 (54·4%) were juveniles, 13 (22·8%) were second-year animals, and 13 (22·8%) were third-year plus animals.

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.

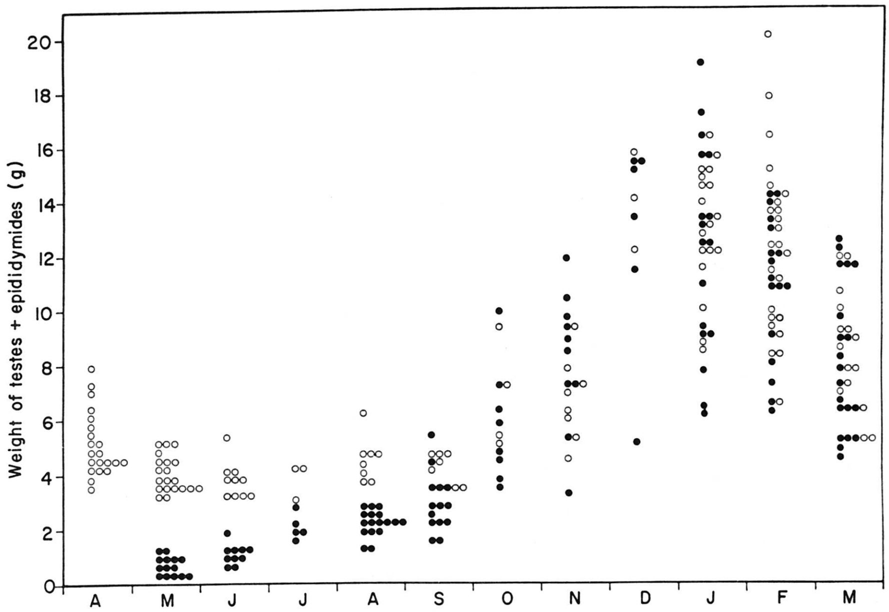

FIG. 3. Growth of the testis with age. Symbols denote: ● juveniles and ○ adult animals.

Use of the eye lens weight in age determination

Introduction

Like other ectodermal structures the eye lens grows throughout life but, because of its unusual position in the body, little if any of this additional lens material is worn away, thereby, at least in theory, resulting in a steady increase in size (Morris, 1972).

Eye lens weight has been used as a means of age determination in relatively few species of canids. Lord (1961) examined the lenses of 104 Gray foxes (*Urocyon cinereoargenteus floridanus*). He found that there was 78% agreement between lens weight and tooth wear techniques when both were used to estimate age, and that there was 90% agreement when the two techniques were simply used to distinguish between juvenile and adult foxes. 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, but did not prove, that each peak represented an age class. Lombaard (1971) examined the lenses of 64 known-age *Canis mesomelas*, and found that the eye lens weight was only useful in separating jackals less than 30 weeks old from older animals.

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

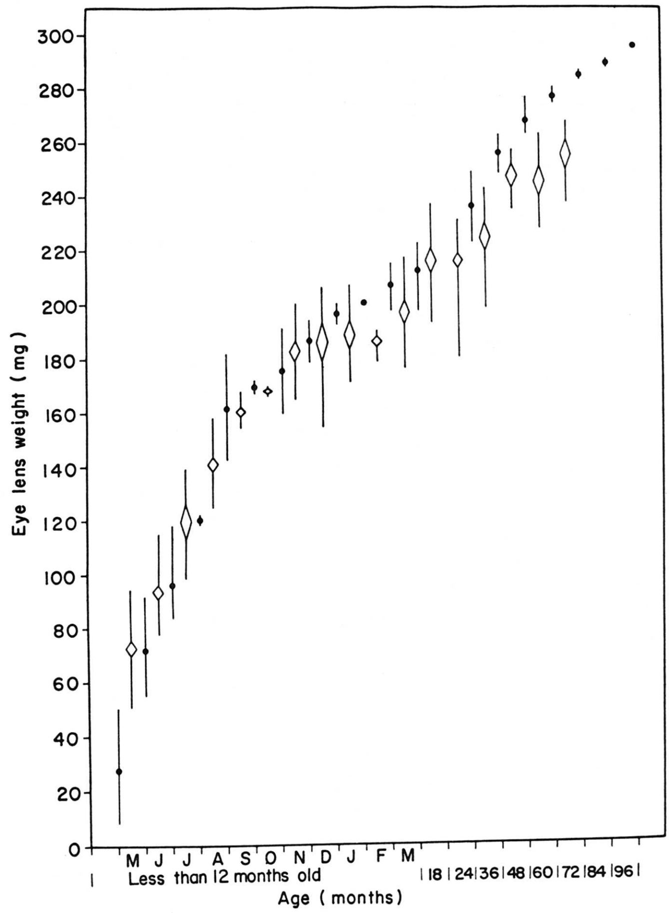

FIG. 4. Increase of the eye lens weight with age, comparing data from the present study (lozenge) with that of Haaften (1970) (black dots). Vertical lines denote the range of recordings, lozenges show the standard error for the London data and black dots mark the means recorded by Haaften.

juveniles could be separated from adults by this technique with "a high degree of accuracy", but that separation of age groups among adults appeared remote. Phillips (1970) used the technique with success to study the annual recruitment of young foxes into the adult population. The sample was collected between late October and December, and only 2·8% of the lenses fell in the transition range between juveniles and adults (210–219 mg). When Johnston & Beauregard (1969) applied 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 the specimens before fixation in the laboratory; they abandoned the technique. In contrast, Haaften (1970), using the dried eye lens weight, was able not only to separate juveniles from adults but also to age the adults, finding almost total separation of year classes for animals up to eight years of age (Fig. 4). At the other extreme, Ryan (1976) found that in foxes from New South Wales the eye lens weight was not even suitable for distinguishing between animals under one year old and those older than a year. The usefulness of the technique for the Red fox is subject therefore to some debate. Storm *et al.* (1976) gave details of eye lens weights in five colour phases of known-age captive Red foxes, these samples all being taken in November.

Preparation of eye lenses

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

(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 half-inch slit was made at the back of the eye 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) The lenses were cooled in a dessicator over anhydrous calcium chloride and only removed briefly, when cool, for weighing.
(6) For age determination purposes only lenses with no external signs of damage were used, and the two lenses had to differ in weight by only 1% or less. A large number of animals were shot in the head, so that one of the eyes was damaged. In these cases the remaining lens was used if it showed no external signs of damage, but less reliance was placed on the results so obtained.

Results and discussion

144 pairs of lenses differing in weight by 1% or less and 30 single undamaged lenses were prepared. The growth of the eye lens with age is shown in Fig. 4—since no sex difference was found both sexes were treated together. There is a complete separation of juveniles from older animals up to the end of September. During the winter months (October to March) only one out of 43 animals (2·3%) less than a year old had an eye lens weight in excess of 210 mg (217·3 mg) and this weight was taken as the separation point between juveniles and adults. In the three month sample October to December, 21/23 (91%) of the animals with an eye lens weight less than 210 mg were less than a year old, and for the January to March

sample, 21/25 (84%) were less than a year old. Thereafter there was a complete overlap of year classes. Friend & Linhart (1964) also found that the separation of juvenile from adult Red foxes occurred with an eye lens weight of 203 to 213 mg; it is interesting to note the same separation point of eye lens weights in both London and American foxes when the two samples differ in total body weight (Harris, 1975). 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. Their sample, however, was only collected in September and October, and the same success in separating juveniles from adults in the late autumn was found in the present study, but later in the winter less reliable results were obtained; with their sample limited to only a few months of the year, Friend & Linhart over-estimated the value of the technique.

The data presented by Haaften (1970) for foxes from the Netherlands is interesting; why he obtained such good results is difficult to explain and unfortunately no details of the sample are given. Haaften's results are contrary to those of Friend & Linhart (1964), Ryan (1976) and the present study, and Brömel & Zettl (1974) were not justified in using Haaften's data to age their sample from North Hesse without first proving its reliability for their population.

Use of tooth wear in age determination

Introduction

Tooth attrition is one of the oldest techniques for age determination, being particularly applicable to large herbivores. Spinage (1973) noted that the pattern of attrition should tend to follow a negative exponential rate of wear, so that a rapid rate of wear in younger classes makes them look older, whilst flattening of the curve in the older classes makes them difficult to separate from the younger ones.

In the canids, Gier (1968) aged *Canis latrans* using wear of the upper and lower incisors and canines, and included a diagram showing the degrees of wear in animals up to eight years of age. He made no attempt, however, to demonstrate the accuracy of the 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 *Canis mesomelas* and found that in two-year old animals the first signs of wear started to appear on I^1 and I^2, while in animals seven years of age and over no cusps or fissures remained; in some animals the teeth were worn down to the gum line and this technique could not be used for animals over seven years of age. Gurskii (1973) noted that in *Canis lupus* 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.

Wood (1958) aged the Gray fox (*Urocyon cinereoargenteus*) by tooth attrition, the character selected being 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, and for 44 known-age readings he found a 93·2% correlation with estimated age. Markina (1962) described the sequence of wear of the teeth of the Red fox, the incisors showing the first signs of wear, which appeared at about one year of age. Stubbe (1965) modified the scheme of Wood (1958) and applied it to the Red fox, recognising four distinct age classes based on molar wear for his material, which was sampled in the autumn only, 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 in 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.

Recording tooth attrition

A variety of teeth were originally examined for tooth attrition in all animals over six months of age; prior to that age the milk teeth are still being replaced by the adult dentition (Markina, 1962; Linhart, 1968; Haaften, 1970; Lüps *et al.*, 1972; present study). It soon became apparent that the canines, premolars and carnassials were so easily broken that they were of little use in age determination, and so only the upper incisors and first upper molar were examined in detail; the lower incisors were worn too rapidly to be of use in age determination. The degree of attrition of the upper incisors was marked on a card showing the outline of the unworn teeth. Molar wear was recorded using the standards of Wood (1958).

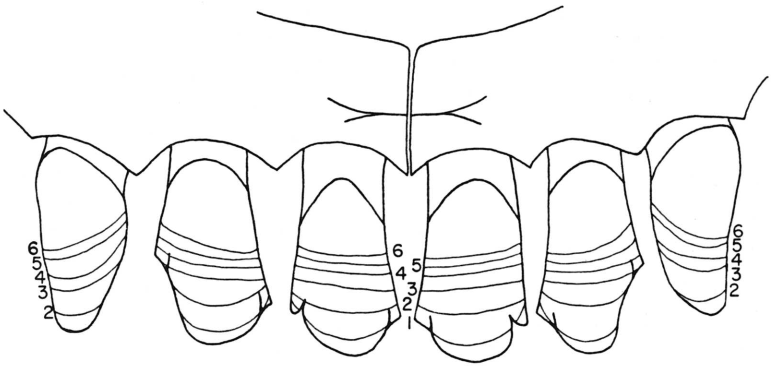

FIG. 5. Average rate of annual attrition of the upper incisors of winter-killed suburban foxes, up to six years of age. The figures refer to the year class.

Results and discussion

Tooth wear proved to be of 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 individual food preferences. The average degree of incisor wear in winter-killed animals is shown in Fig. 5, the lines denoting the amount of wear expected for each year class up to six years of age. Summer-killed animals show a degree of wear intermediate between the winter samples.There was considerable 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 more marked on 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 Fig. 5, and 93·3% of the sample up to four years of age were aged with only one year error or less. With increasing age the amount of additional tooth wear each year was less, so that the percentage accuracy of this technique diminished

(Tables III and IV). The technique was most useful in separating those juveniles which still exhibit a marked *fleur-de-lys* pattern to the upper incisors, this disappearing by the second year. Brömel & Zettl (1974) found that incisor wear was "useful" for ageing German animals up to two years of age but that thereafter exact age determination was not possible. The use of molar wear for age determination was considerably less reliable, showing a greater degree of variability than incisor wear, the converse of the results obtained by Wood (1958) for *Urocyon*. There was a marked tendency to over-estimate the age of first year winter-killed animals (Table V), with only about half the second and third year animals correctly aged, but with one year error or less almost exactly the same accuracy (92·5%) was obtained as with incisor wear (Table VI). Greater accuracy was not obtained if the sample was limited to any one time of the year.

TABLE III

Effectiveness of upper incisor wear in the determination of age in 165 winter (October–March) killed animals

		Age estimated from upper incisor wear (Fig. 5)										
		1st yr		2nd yr		3rd yr		4th yr		older		Total
		No.	%	No.	%	No.	%	No.	%	No.	%	
Objective age	First year	65	73	20	23	3	3	1	1			89
	Second year	11	23	31	65	4	8	1	2	1	2	48
	Third year			6	33	8	44	3	17	1	6	18
	Fourth year			4	40	1	10	4	40	1	10	10

TABLE IV

Accuracy of age determination using incisor wear in 165 winter-killed animals

	Number	%
Age correctly determined	108	65·5
One year error	46	27·8
Two years error	9	5·5
Three years error	2	1·2
Total	165	100·0

Stubbe (1965) did not demonstrate the accuracy of molar wear for age determination in the Red fox, but Bree, Chanudet *et al.* (1973) found a 35% accuracy with 79 foxes from the Netherlands and 47% with 97 foxes from France, with most errors not exceeding one year. With 227 London 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 differing environments is interesting, especially since one might expect a marked variation in tooth wear in relation to the nature of the food. Despite these similarities age criteria based on tooth attrition should not be randomly applied to differing populations without first referring to known age material.

TABLE V

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										
		1st yr		2nd yr		3rd yr		4th yr		older		Total
		No.	%	No.	%	No.	%	No.	%	No.	%	
	First year (October–March)	28	31	54	60	6	7	2	2			90
	Second year	7	8	47	52	31	34	5	6			90
Objective age	Third year	1	3	6	19	15	47	10	31			32
	Fourth year			3	20	7	46	4	27	1	7	15

TABLE VI

Accuracy of age determination using first upper molar wear in 227 animals sampled throughout the year

	Number	%
Age correctly determined	94	41·4
One year error	116	51·1
Two years error	15	6·6
Three years error	2	0·9
Total	227	100·0

Use of cranial sutures in age determination

Introduction

Cranial sutures have been used to determine the age of some canids. Wood (1958) found that in the Gray fox most of the skull sutures were closed by January in their first year. Dolgov & Rossolimo (1966) found that in the Arctic fox the basioccipital and sphenoid suture was closed even in animals only 6–10 months old, and in animals 10–12 months old the basisphenoid and presphenoid suture and a variety of other sutures were ossified. Macpherson (1969) also found these sutures to be open or visible in *Alopex* up to a year old. Gurskii (1973) found that for the wolf the sequence of closure was the same as that described for other canids but that the rate was much slower e.g. the basisphenoid and presphenoid suture started to close in the fourth year and was completed in the sixth year.

Churcher (1960) devised a key for ageing the skulls of Red foxes, using crania from 188 known-age farm animals and 1288 wild crania, based largely on suture closure. His key is based on the assumption that the sutures close in a set order and at precise ages. But Johnston & Beauregard (1969), using the same 188 known-age crania as reference material, came to different conclusions, and noted that suture closure was excellent for distinguishing animals in their first two years of life, but that there was no way of accurately separating three and four year old animals by this technique. Markina (1962) also examined the sutures of 166 crania from Russian Red foxes, and found that in animals 6–12 months old the basioccipital–basisphenoid suture was closed, but since he had no criteria by which to age older skulls he was unable to comment further on suture closure.

Preparation of crania

Most crania were prepared by allowing the entire corpse to decompose, after which the skulls were bleached in a hot solution of sodium perborate (Chapman & Chapman, 1969). A few crania were defleshed by gentle boiling, and then bleached in the normal way. Sutures were scored as open, closing or closed.

TABLE VII

Closure of the basioccipital-basisphenoid 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
Total	46	42·6	20	18·5	42	38·9

Results and discussion

A variety of sutures were examined, particularly those sutures used by Churcher (1960) in his key. Many sutures closed irregularly and proved to be of little use in age determination. The most useful suture was that between the basioccipital and the basisphenoid (BOBS). This suture began to close in some cubs as early as June, the first fully closed sutures appearing in October, and being closed in all animals by January (Table VII).

For a three-month sample October-December 12/26 (46·2%) did not have the suture closed and so could be recognized as juveniles on this character alone. Those with the BOBS suture closed still had the presphenoid-basisphenoid suture (PSBS) open or only just starting to close and this character delimited them as first year animals. As Table VIII shows the PSBS suture started to close in a few animals 7–9 months old (3·6% of the October–December sample), and in 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. In most animals, however, this suture closed progressively during the second year of life, so that during the period April–December this suture would characterise second year animals if it was open or closing but, if closed, the animal could belong to any year class from the second upwards. This character allowed recognition of 36/53 (67·9%) of the second year

TABLE VIII

Closure of the presphenoid–basisphenoid suture in 200 animals six months to three years old

Year class		Open No.	Open %	Closing No.	Closing %	Closed No.	Closed %
First year:	Oct.–Dec.	27	96·4	1	3·6		
	Jan.–March	55	90·1	4	6·6	2	3·3
Second year:	April–June	23	71·8	6	18·8	3	9·4
	July–Sept.	3	42·9	1	14·2	3	42·9
	Oct.–Dec.	2	14·3	1	7·1	11	78·6
	Jan.–March			6	20·7	23	79·3
Third year:	April–Dec.					16	100·0
	Jan.–March			2	15·4	11	84·6

animals up to the end of December, but 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 be first, second, or possibly third 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 IX). This suture first started to close in a few animals as they entered their third year, the first fully closed suture appearing in an animal at the end of its third year. This suture closed progressively during the fourth and fifth year classes, and was fully closed by the sixth year in all animals.

No other suture provided even remotely useful data for age determination. Features such as the change in shape of the post-orbital processes and the formation of the occipital and sagittal crests proved to be very irregular and, although such changes are associated with ageing, the rate of change is not quantifiable.

As can be seen the individual rate of suture closure is very variable, and in a wild population it is completely impossible to assign set ages to the time of closure, as did Churcher (1960) for his captive bred animals. One possible explanation for these differing results is that Churcher's 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. When Churcher's key is applied to London's fox population it tends to over-estimate age, usually by one year in younger animals and by three to five

TABLE IX

Closure of the lateral palatal portion of the premaxillar–maxillary suture in 59 third to sixth year animals

Year class	Open No.	Open %	Closing No.	Closing %	Closed No.	Closed %
Third year	24	77·4	6	19·4	1	3·2
Fourth year	3	25	6	50	3	25
Fifth year			4	40	6	60
Sixth year					6	100

years when considering the closure of the PMMS. Johnston & Beauregard (1969) suggested that this technique "was excellent for distinguishing animals during the first two years of life". This was not the case in the present study, the suture technique only allowing reliable recognition of 67·9% of the second year animals up to the end of December, and no second year animals thereafter. Also Johnston & Beauregard found that none of their animals from Ontario showed a fusion of the PMMS, although the oldest animal was 51 months old, whereas in the present study all animals at this age had the suture closing or fully closed. It would appear that the rate of suture closure is greater in London foxes than those from Ontario.

Use of epiphyseal closure in age determination

Introduction

The epiphyses of a mammal remain cartilaginous during the period of growth, and become ossified when adult size is attained. Several longitudinal studies of epiphyseal fusion have been made for various breeds of Domestic dog (Seoudi, 1948; Pomriaskinsky-Kobozieff & Kobozieff, 1954; Bressou *et al.*, 1957; Smith, 1960; Smith & Allcock, 1960; Hare, 1961; 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, when considering 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; their paper gives full details of the sequence of changes in the dog. All epiphyses were fused by about eighteen months of age. 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 thought to be the same species. This is the converse of the situation seen in goats (Noddle, 1974). Lombaard (1971) found that in *Canis mesomelas* 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 *Alopex lagopus beringensis* and found that ossification of the skeleton terminated at the age four to six months. Growth of the peripheral skeleton was completed before growth of the axial skeleton. However, in Canadian *Alopex* Macpherson (1969) found that the epiphyses of the long bones were still open in whelps killed in November and December, when over six months old. Sullivan & Haugen (1956) X-rayed the lower radius and ulna of young captive Red and Gray foxes, and found that animals could be classified as juveniles or adults through November, and some were distinguishable through most of December. Reilly & Curren (1961) showed by means of X-rays that the proximal epiphysis of the humerus closed at 9–9½ 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 in February. They showed that the proximal epiphysis of the tibia remained open for the same period of time, and suggested that the technique was 100% reliable up to the end of November.

Recording epiphysis data

Originally epiphyseal closure was recorded for each animal both by means of X-ray plates and cleaned bones, prepared by allowing the corpse to decompose and then bleaching the bones in a hot (not boiling) 2·5% solution of sodium perborate. Both techniques yielded the same results, and so for the majority of specimens cleaned bones only were used, although the epiphyses in the feet were always recorded by means of X-ray plates.

Eight animals (four of each sex) from three different litters were raised in captivity, X-rayed and later killed at set dates to confirm the approximate rate of epiphyseal closure. The rate of tooth eruption (Haaften, 1970) was used to age the cadavers of wild cubs.

Results and discussion

For the first three weeks of life no data are available on epiphyseal closure. Thereafter the sequence of closure is shown in Table X; the bones of the feet ossify by 22 weeks of age, those of the vertebral column by 27 weeks, and the limb bones (excluding the apophysis) by 30 weeks. After that the cartilaginous borders of the scapula, ilium and ischium ossify, and the symphysis pubis and symphysis 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. It must be noted that the time of closure recorded for each epiphysis is an average, and that within a litter of cubs killed in June there will be a range of developmental stages, with up to four weeks separating the least and best developed animals in the same litter. Ballenberge & Mech (1975) recorded similar variations in development within litters of wolf cubs. As a result, epiphyseal closure is most accurate when used for aging a whole litter of cubs rather than individual animals.

During the autumn and early winter only one epiphysis is of use for separating juveniles from adults, this being the fusion of the apophysis with the diaphysis of the tibia (Table XI). This closes slowly during the autumn, starting in October, being fully closed in a few animals killed in November, and in 90·9% of the first year animals killed in February.

The epiphyses of the Red fox close rapidly, so that most changes are complete by the time the animal is seven months old; this rate of closure is faster than American authors have recorded, e.g. Sullivan & Haugen (1956) recorded that ossification of the distal epiphysis of the radius and ulna was completed in foxes 8–9 months old, and Reilly & Curren (1961) found that the proximal epiphysis of the humerus remained open until 9 or 9½ months. Jensen & Nielsen (1968) found that in Danish foxes after fusion of the proximal epiphysis of the radius and the thickening of the bone had disappeared, it was possible to distinguish *most* first year animals from older animals up to January by surface changes in the bone, although this did require comparative skeletal material of known age. This suggests a rate of epiphyseal closure similar to that recorded in the present study, and a faster rate than was recorded by American authors.

Conclusions

In the canids that have been studied the sequence of growth changes is very similar, the epiphyses and sutures closing in similar sequences, and tooth wear and growth also following similar patterns. The average rate of developmental changes recorded for each species depends on the size of the animal, being greater in the smaller, shorter-lived species. Thus the sutures are fully closed in the sequence *Urocyon cinereoargenteus*, *Alopex lagopus*, *Vulpes vulpes* and *Canis lupus*, and epiphyses in the sequence *Alopex lagopus*, *Vulpes vulpes*, *Canis mesomelas*, *Canis familiaris dingo* and *Canis familiaris*. Similar patterns can be drawn for other growth parameters; current knowledge should allow a rough evaluation of

TABLE X

Ages at which the epiphyses close in Red fox cubs. Based on data from 8 captive and 20 wild cubs.

Approximate month		April				May				June				
Age in weeks	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Epiphyses of fore and hind feet (carpal and tarsal bones omitted).										Epiphysis medial phalanges, forefeet	Epiphysis medial phalanges, hindfeet			Fibular tarsal epiphysis closes
Epiphyses of vertebral column		No data available for first three weeks of life		Body cervical 3–7 Body thoracic 12+13 Body lumbar 1–7 Body sacral 2+3		Body of axis Body thoracic 1+11 Body sacral 1	Body thoracic 2	Body thoracic 3, 4, 10	Dorsal arch+ventral plate of atlas Pars lateralis of sacrum	Body thoracic 5–9				
Epiphyses of limbs and girdles							Medial epicondyle of humerus fuses to epiphysis Medial malleolus of tibia ossifies	Ischium–pubis ossify		Tuber scapulae ossifies	Os acetabulum, ilium–ischium+ilium–pubis ossify			

July					August					September				October	
15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
	Epiphysis proximal phalanges, forefeet														
		Epiphysis proximal phalanges, hindfeet													
				Epiphysis metacarpals											
					Epiphysis metatarsals										
		Odontoid process of axis						Cranial epiphysis cervical 6+7	Cranial epiphysis cervical 3–5		Caudal epiphysis of axis				
				Cranial epiphysis sacral 1–3			Caudal epiphysis sacral 1–3	Cranial epiphysis thoracic 1–8, 12, 13	Cranial epiphysis thoracic 9–11		Caudal epiphysis cervical 3–7				
				Cranial epiphysis coccygeal 1–4	Cauda epiphysis coccygeal 1–4			Cranial epiphysis lumbar 1+7	Cranial epiphysis lumbar 2–6	Caudal epiphysis lumbar 1–6	Caudal epiphysis thoracic 1–5, 12, 13				
									Caudal epiphysis lumbar 7			Caudal epiphysis thoracic 6–11			
					Cranial epiphysis coccygeal 5–20				Caudal epiphysis coccygeal 5–20						
		Distal epiphysis humerus								Greater trochanter of femur ossifies			Distal epiphysis radius + ulna		Cartilage vertebral border of scapula ossifies
		Medial epicondyle humerus fuses to diaphysis							Distal epiphysis of tibia				Proximal epiphysis femur	Proximal epiphysis humerus	
		Proximal epiphysis ulna			Proximal epiphysis radius				Distal epiphysis of fibula		Distal epiphysis of femur		Lesser trochanter of femur ossifies		Iliac ischiac cartilages of os coxa ossify
		Apophysis of tibia fuses to epiphysis											Proximal epiphysis tibia + fibula		Apophysis closes

TABLE XI

Date of closure of the apophysis in 202 animals less than 18 months old

		Open		Closing		Closed	
		No.	%	No.	%	No.	%
First year	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
Second year	May					12	
	June					6	
	July					2	100
	August					4	
	September					1	

the suitability of present age determination techniques when commencing a study on a new species of canid.

Within the species variations in rates of development also are apparent when comparing different fox populations, so that it is important to ensure the validity of a technique before applying it to a new population. For instance, suture closure in Ontario Red foxes occurred at a more protracted rate than was found in London foxes, and the rate of epiphyseal closure in American foxes was also slower than in Danish and London foxes, so rendering the technique more useful in America for separating juvenile from adult animals.

When examining age determination techniques in the Mule deer (*Odocoileus hemionus*) 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 is often a subjective estimate due to variables such as the teeth on one side being badly worn, while those on the other side show little wear, missing teeth producing 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 there was a close correlation between the interpretations of an experienced and an inexperienced recorder. The tooth sectioning technique suffers the main disadvantage in being time consuming, although once the material has been collected and decalcified a large number of sections can be prepared in a relatively short period of time.

The other age determination techniques were examined in an attempt to save the unnecessary sectioning of teeth from juvenile animals killed in their first winter. Few of the techniques examined were of value even in this limited respect. The simplest technique considered to be absolutely reliable in London foxes is to cut the canine tooth transversely with a hack-saw; if the pulp cavity is pronounced, about half the width of the tooth or more, the animal is a juvenile. A variety of techniques will separate a proportion of the juveniles in a winter sample. These include an open apophysis, an unfused basioccipital-basisphenoid suture, and a *fleur-de-lys* pattern to the upper incisors, but these techniques all suffer from the serious drawback in that they cannot be used to recognise *all* the juvenile animals, and so by themselves cannot be used even to calculate the annual recruitment to the adult population. The technique of Allen (1974) suffers from the same drawback.

None of the measures of growth (baculum weight, eye-lens weight, skull and skeletal measurements) proved of any absolute value for age determination in the present study, although some measurements such as baculum weight and eye-lens weight can be a guide to the approximate age of an adult animal, helping in the interpretation of poorly defined annuli in the tooth cementum. This also applies to suture closure and incisor wear, which allow a broad age grouping of the specimens. Eye-lens weight seems to be a useful measure for some Red fox populations, Haaften (1970) claiming separation of year classes and Phillips (1970) used it to study annual recruitment of juveniles to the early winter population. Eye-lens weight could be used for a similar study of London foxes, with an accuracy of 91%, but was much less reliable in a late winter sample.

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