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High incidence of malocclusion in an isolated population of the red fox (*Vulpes vulpes*) in the Netherlands

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(With 2 plates and 4 figures in the text)

Out of 72 fox skulls (*Vulpes vulpes* L.) collected in the North Holland Dune Reserve (NHD) between 1979 and 1985, 12 (16·7%) skulls showed a pronounced protrusion of the maxillary incisors over the mandibular incisors. Comparison of dimensions of affected and normal skulls revealed that this protrusion was the effect of a shortening of the front part of the mandibles. The mode of inheritance of this aberration is thought to be under recessive monogenetic control. This was deduced from the family relations between individual foxes radio-collared or earmarked during five years of ecological research, and from the clear bimodal distribution in mandible length. The high incidence of the aberration can be explained by the history of the fox population in the NHD. Before 1968 the NHD was not inhabited by foxes as a result of its ecological isolation. It is rumoured that in that year four cubs, probably from one litter, were set free. It is believed, therefore, that the present population has originated from a small and isolated gene pool. Compared to normal foxes, affected animals are likely to be at an ecological disadvantage. Hence it is expected that the incidence of the aberration will decline in the future, since the population density reached a stable maximum around 1982 and the selective forces against the aberration will presumably be stronger now than during the phase of rapid population growth.

Contents

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Introduction

Until 1968 the 3–5 km-wide strip of sand dunes along the western coast of Holland was not inhabited by foxes. It is believed that the vast area of low-lying wet meadows in the western part of Holland constituted an ecological barrier for foxes. Between 1936 and 1968 only five foxes are known (from press reports) to have been shot or observed in or near the dunes; these were young dispersing males originating from fox populations at least 60 km to the east, or foxes escaped from captivity. These foxes were all caught in the southern half of the dune strip; the northern part of the dunes is geographically even more isolated (Fig. 1), being separated by a channel 250 m wide with only one crossing point (a chain of bridges in a built-up area).

From 1968 onwards, an increasing number of fox sightings was reported from both the southern and the northern part of the dunes. An anonymous person has told us that in 1968 four young foxes, presumably cubs from the same litter, were introduced into the northern part of the dunes, the North Holland Dune Reserve (NHD). By 1975, foxes were common in the area and in 1979 a fox research project was initiated by the Waterworks of the Province of North Holland, the company in charge of the nature management of the NHD. This study (until 1985) focused on the population ecology of the fox and its role as a predator of birds. Some preliminary findings can be found in Mulder (1985*a*, *b*).

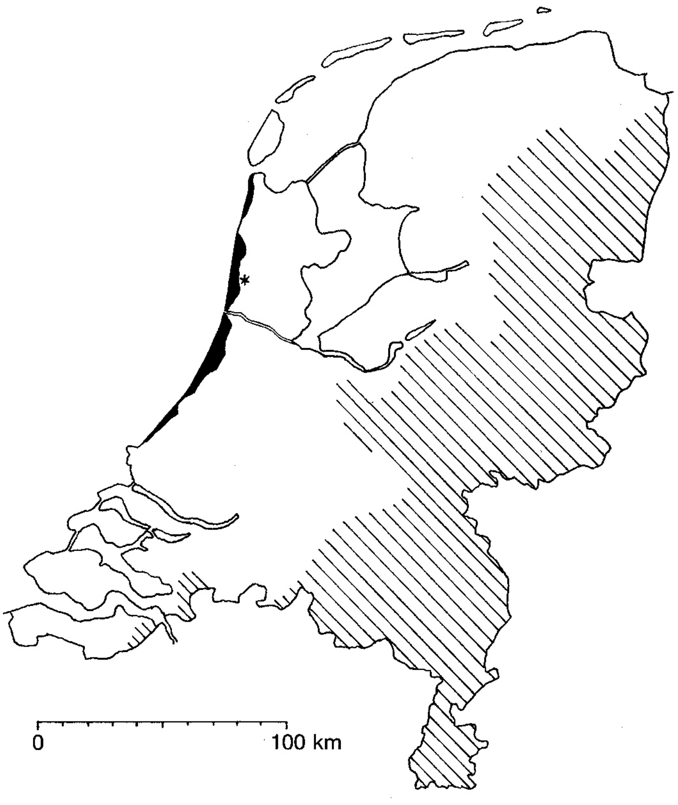

FIG. 1. Distribution of the red fox in the Netherlands until 1968 (▧), and occurrence since then along the western coast (■). The location of the study area is indicated with *.

During fieldwork, it was noted that some of the captured foxes could not close their mouths in a normal way. It was possible to study this aberration in more detail when many fox skulls became available from this area in the course of the years. The population research provided knowledge about the family relations of foxes with and without the aberration, giving a unique opportunity to help explain the mode of inheritance of the phenomenon.

The high frequency of missing or supernumerary teeth in foxes and other canids is well known (see for instance Fleischer, 1967, and van Bree & Sinkeldam, 1969). Therefore the possible relation between aberrations of skull and dentition was studied as well.

Methods

Terminology

In the available literature, there is no uniformity in the terminology for skull aberrations in which the mandible is disproportionate to the rostrum. This is because the situation is complex: both the dimensions of the skull itself and the dental occlusion, i.e. the relative position of the upper and lower teeth, are involved. In many papers the specific terms used for forms of malocclusion are not clearly defined, and often it is not possible to judge how much skull features and tooth positions contribute to the overall effect. Examples of terminology applied to malocclusions in which there seems to be a difference in length between upper and lower jaw are 'protrusion of the mandibular or maxillary incisors' (Colyer, 1936) and 'mandibular or maxillary prognathism' (Björk, 1969). Solow (1980) applied the same terms Björk used, as well as 'mandibular or maxillary retrognathism'. The terms 'retrognathism' and 'prognathism', however, are exclusively used in studies on the human skull, describing the position of the jaws in relation to the forehead. Other terms frequently used are 'overjet' and 'overbite', mostly applying to the relative position of the incisors only.

To avoid all problems of terminology we decided to use just the general term 'malocclusion' for the aberration found in our material. The exact nature of the aberration will become clear in the **Results** section.

Material and measurements

Between 1979 and 1985, many foxes were found dead in the 3600 ha study area in the NHD, almost invariably victims of poisoning by poachers. Of the collected skulls, a total of 72 (34 males, 28 females, 10 of unknown sex) could be studied. These skulls were examined for missing and supernumerary teeth and checked for malocclusion. From all skulls with permanent dentitions, including two with incomplete permanent dentitions, the following measurements were taken to the nearest 0·1 mm: condylobasal length (Cbl), mandible length (Mand) and palate length (Pal) (Fig. 2). In addition, two measurements were taken from the frontal parts of the skull: in the upper jaw, the distance between the front of the maxilla (prosthion) and the anterior margin of the socket of the carnassial tooth P^4; in the lower jaw, the distance between the front of the mandible (infradentale) and the anterior margin of the socket of the carnassial tooth M_1 (for definitions, see Duerst, 1926). These measurements are referred to as upper muzzle length (UM) and lower muzzle length (LM), respectively, for convenience. In skulls with milk teeth corresponding measurements were obtained from the distance between the tip of the jaws and the P4 in both upper and lower jaw.

Not all measurements could be obtained from all skulls, owing to missing or damaged parts.

Two ratios were used: mandible length/condylobasal length (Mand/Cbl ratio) and palate length/condylobasal length (Pal/Cbl ratio). Except for extremely young animals, these ratios proved to be independent of skull size, so they can be used to reflect aberrations in the growth of the mandible or palate, irrespective of the age of the animal.

Most of the fox skulls studied form part of the collection of the Amsterdam Zoological Museum; a few are in private collections.

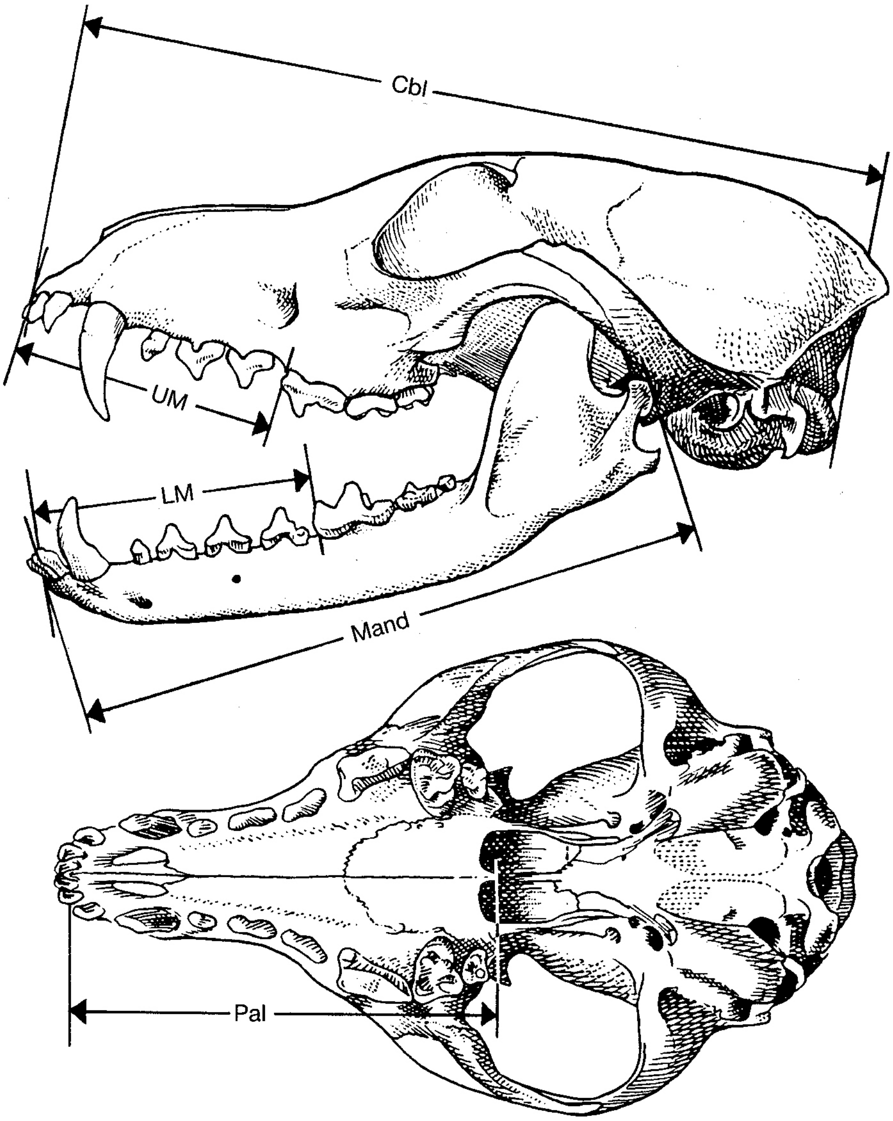

FIG. 2. Indication of the measurements taken from the fox skulls (see Duerst, 1926): Cbl, condylobasal length (condylus occipitalis, prosthion); Mand, mandible length (condylium mediale, infradentale); Pal, palate length (staphylion, prosthion); UM, upper muzzle length (anterior margin of the socket of P^4, prosthion); LM, lower muzzle length (anterior margin of the socket of M_1, infradentale). These last two measurements were taken from both sides of the skull and subsequently averaged. Skull drawings from Lloyd (1977).

Establishing family relations

During the fieldwork of the fox research project, 99 juvenile foxes were earmarked, and additionally 56 adult and juvenile foxes were fitted with radio-collars. No systematic attention was paid to the teeth, but in some individuals a malocclusion was noted. The foxes appeared to form stable family groups, consisting of 1 male and 1–3 females sharing a territory (Mulder, 1985*a*). In several adjoining territories, almost every adult fox was radio-collared. Individual foxes were followed for periods ranging from several months up to 3·5 years. Cubs of the radio-collared females were caught and earmarked at the dens, which generally enabled irrefutable mother-young relations to be determined. Sometimes, however, 2 vixens attended the same litter, or 2 litters were present at the same den, obscuring the exact relations between individuals. Although no

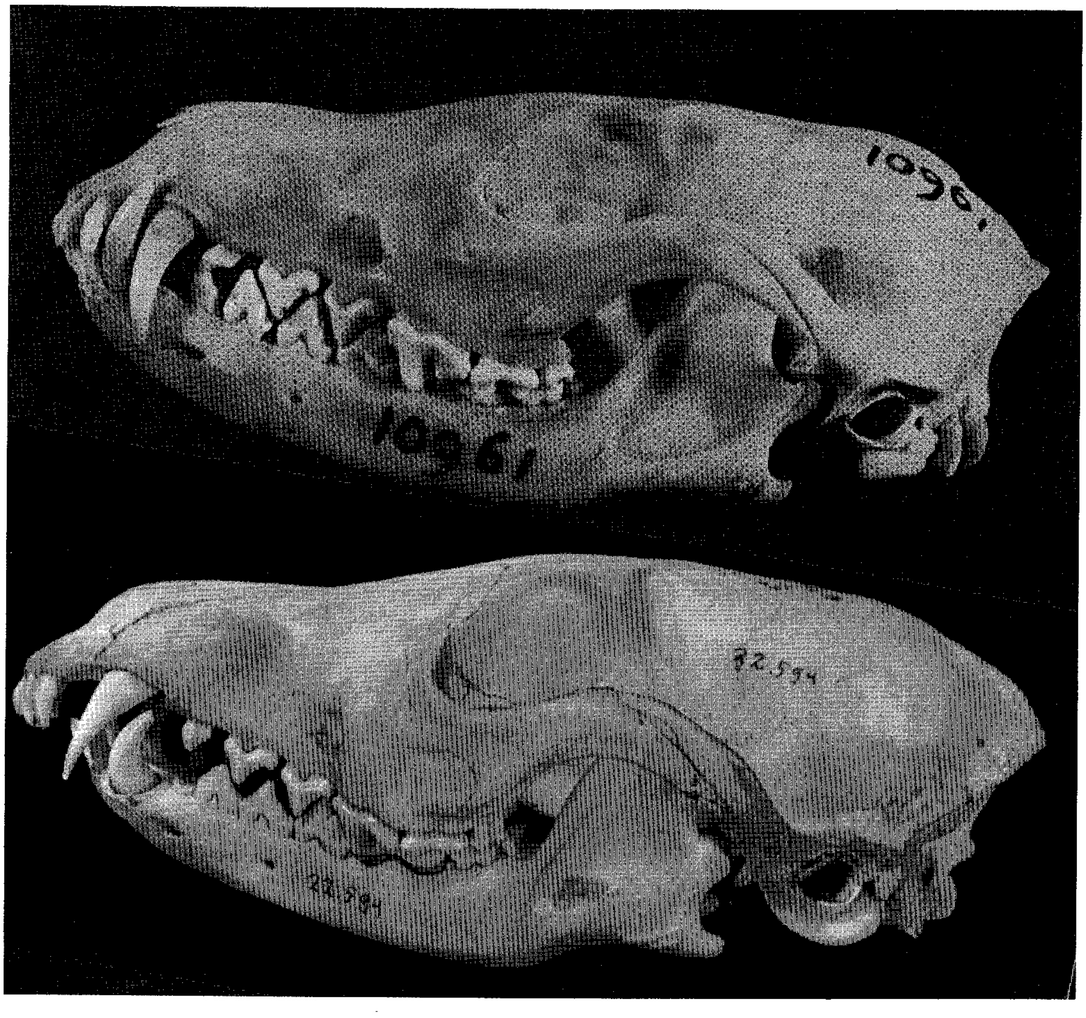

PLATE I. Fox skull with normal occlusion (above) and with the malocclusion as described in this paper (below).

actual matings were observed, it was assumed that the male territory holder was the father of the cubs of the alpha female, because the male follows the alpha female closely during the few days of her oestrus (MacDonald, 1980). Cubs of beta females were not attributed to the male in their territory; there are indications that beta females may copulate with males from neighbouring territories or with non-territorial males (Niewold, 1980).

Results

Frequency and nature of the anomaly

In 12 (five males, three females and four of unknown sex) of the 72 fox skulls (16·7%), the rostral part of the skull was protruding abnormally far over the mandibles (Plate I). At least six (four males, two females) other foxes, from which the skulls were not subsequently collected, showed this aberration at the time of live capture (Plate II).

In many cases the malocclusion was particularly obvious from the relative position of the upper and lower canines. In a normal skull the lower canine falls smoothly into the space between the third upper incisor and the upper canine. In the aberrant skulls a variety of positions of the lower canine was noted, presumably as a result of the chance situation of the tips of both canines relative to each other during their growth. Many of the lower canines clearly had been forced to grow into a tilted position to one side of the upper canine, often resulting in heavy lateral wear of both canines.

PLATE II. Young fox (aged 5 months) with malocclusion, showing the reversed position of upper and lower canine.

TABLE I

The difference (in mm) between the length of the upper muzzle and of the lower muzzle, in normal skulls and in skulls showing malocclusion, for skulls with permanent and milk dentitions

	n	Range	Mean	S.D.
Permanent dentition				
Normal	40	−1·35–4·30	1·90	0·97
Aberrant	9	5·85–9·20	7·97	1·29
Milk dentition				
Normal	14	0·00–3·15	1·15	0·82
Aberrant	3	3·20–5·05	4·25	0·95

For methods of measurement see text and Fig. 2.

Aberrant skulls showed lower canine positions ranging from slightly forward of the upper canine and in close contact with it, to a position completely behind and free of the upper canine. Because of this variation in the relative position of the canines, the aberration may be more reliably detected when looking at the relative position of the incisors. The aberrant skulls always showed a considerable overjet of the upper incisors, resulting in a gap (up to 10 mm) between the upper and the lower incisors, which can also easily be detected in a live fox when viewed from below. This gap itself is, however, not easy to measure in such a way that skulls can be reliably compared, because the degree of wear and tilt of the incisors varies greatly between skulls. For this reason, the difference between upper and lower muzzle length measurements obtained from the skull itself instead of from the teeth, was used as an indication of the gap size (Table I). The results yield an underestimate of the real gap size, as a consequence of the way in which the muzzle was measured: the M_1 is positioned more posteriorly in the lower jaw than the P^4 is in the upper jaw. The variation in gap size between skulls is mainly the result of skull size variation; this absolute measurement is, unlike the Pal/Cbl and Mand/Cbl ratios, sensitive to age.

From Table I it is apparent that the difference between upper and lower muzzle length in aberrant skulls is considerably larger than in normal skulls; the difference is especially clear in skulls with permanent dentitions.

According to the distribution of the Pal/Cbl ratio (Fig. 3), there is no difference in relative palate length between normal and abnormal skulls, whereas the Mand/Cbl ratio shows a clear bimodal distribution with all the abnormal skulls in one group and all the normal skulls in the other (Fig. 3).

This means that the malocclusion is the result of shortened mandibles rather than of an elongated rostrum. When the occlusion in the abnormal skulls was examined, it was invariably found that from the back of the tooth row forward to and including the P^4 and the M_1 (which were always firmly interlocking), the occlusion was identical to that in normal foxes. The difference between normal and abnormal skulls is therefore located in the muzzle region, and the aberration is the result of a shortening of the frontal part of the mandible. In the mandibles of the abnormal skulls, the four lower premolars are compressed in a much smaller space than in the mandibles of the normal skulls; often they touch each other, or are even overlapping, more or less like roofing tiles. As mentioned before, the position of upper and lower canines relative to each other is varied in the abnormal skulls (see next two sections).

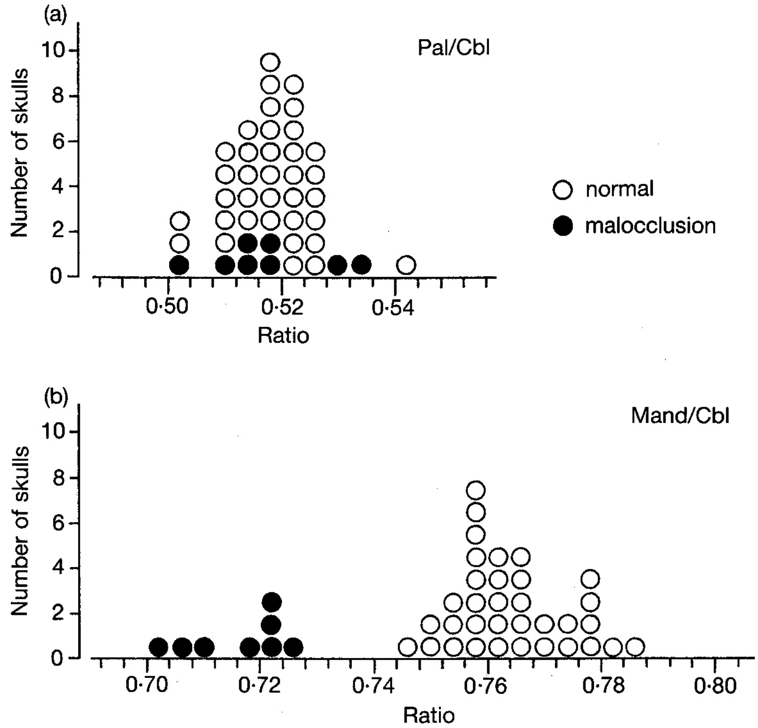

FIG. 3. Distribution of (a) the palate/condylobasal ratio (Pal/Cbl) and (b) the mandible/condylobasal ratio (Mand/Cbl) of the fox skulls studied. For the Mand/Cbl ratio left and right side of the skull were averaged.

Three skulls had to be excluded from the sample, because they did not conform to the clear bimodal distribution in the Mand/Cbl ratio for reasons other than a malocclusion. In one case this was due to a strong sideways curve of the skull, probably the result of an injury or infection in early life; the two other skulls showed a completely normal occlusion, but had shortened mandibles (Mand/Cbl ratio 0·740 and 0·735, respectively) as a result of abnormally small condyles. (condylium mediale).

Effect of occlusion on mandible growth

It is conceivable that the position of the growing upper and lower canines relative to each other is determined by chance in the aberrant skulls, because the bases of the canines are more or less opposite each other. The tip of the growing lower canine may thus fall at any side of the tip of the upper canine. In many of the aberrant skulls the upper and lower canines touch each other in various degrees, generally showing heavy wear. The way in which the canines exert an influence on each other may enhance or diminish the growth of the mandible. In our material there is indeed a clear relation between the relative canine position and the Mand/Cbl ratio of the individual mandible: in 11 mandibles with the canine falling behind the upper canine, the average Mand/Cbl ratio was 0·712 (range 0·698–0·725), in four mandibles with canines falling to the side of the upper canine the average Mand/Cbl ratio was 0·723 (range 0·716–0·726), whereas in one mandible with the canine falling just in front of the upper canine the Mand/Cbl was 0·725. This result is, however, no proof that the position of the canines influences the growth of the mandible, since cause and effect are interchangeable. Only a clear difference in length between the left and right mandible in a single skull with a different position of the canines on either side can be seen as an indication of the existence of such an influence. Two skulls with such a different left and right side were available; the difference between the Mand/Cbl ratios of the left and right side, however, was nil or small; larger differences were found in skulls with similar left and right sides. The same lack of difference between left and right side was found in the measurements of muzzle length. So we can find no indication for an effect of the relative position of the canines on mandible growth.

Disadvantages of the anomaly

Foxes with malocclusion may experience disadvantages in comparison to normal foxes. The position of the lower canines in relation to the upper ones varied in anomalous foxes from anterior to the upper canines (one canine in one skull), through lingual of the upper canines and piercing the palate (seven canines in five skulls), to posterior to the upper canines (12 canines in seven skulls). Of the last group, four lower canines in two skulls were strongly curved backwards and outwards, almost in a horizontal position, and these foxes must have experienced difficulties in getting a grip of prey such as rabbits, the staple food in the dune area (Mulder, 1985*b*). Anomalous foxes with lower canines occluding at the lingual side of the upper canines probably did not have problems in holding prey, but must have felt a physical inconvenience, in view of the deep impression the lower canines caused in the palate.

Although in anomalous foxes the occlusion of the canines is far from normal, and many lower canines impinge on the upper canines, no statistical difference was found in our material, as regards the number of broken canines, between normal and abnormal skulls. In anomalous foxes, 20·0% of all upper canines ($n=20$) were broken off for more than half of their original length, whereas in normal foxes 16·3% of all canines ($n=86$) were broken off ($\chi^2=0{\cdot}16$; $P>0{\cdot}1$). Corresponding figures for the lower canines were: 0·0% in anomalous foxes ($n=20$), and 14·8% in normal foxes ($n=88$; $\chi^2=3{\cdot}36$; $0{\cdot}1>P>0{\cdot}05$). In abnormal skulls, some of the canines which had not broken off showed slight to heavy wear, as a result of touching the opposite canine. However, canines in normal skulls often showed the same kind of wear in light to moderate degree as well.

Missing and supernumerary teeth

A statistical comparison of the number of missing teeth in the mandibles of anomalous and normal foxes revealed no significant differences. In anomalous foxes 10·0% of the total number of P_1 were missing, in normal foxes 4·1% ($n=141$; $\chi^2=1{\cdot}25$; $P>0{\cdot}1$); in all skulls 5·0% of the total number of P_1 were missing, these losses involving 8·3% of the skulls. Figures for the M_3 were: anomalous foxes 6·3% missing, normal foxes 9·8% ($n=128$; $\chi^2=0{\cdot}21$; $P>0{\cdot}1$); in all skulls 9·4% of the total number of M_3 were missing, involving 12·5% of the skulls.

In addition one P^2 was missing in a normal skull, and in one (abnormal!) skull an extra upper premolar was present between the P^1 and P^2.

Hereditary transmission of the anomaly

The established family relations between foxes with and without the malocclusion are shown in

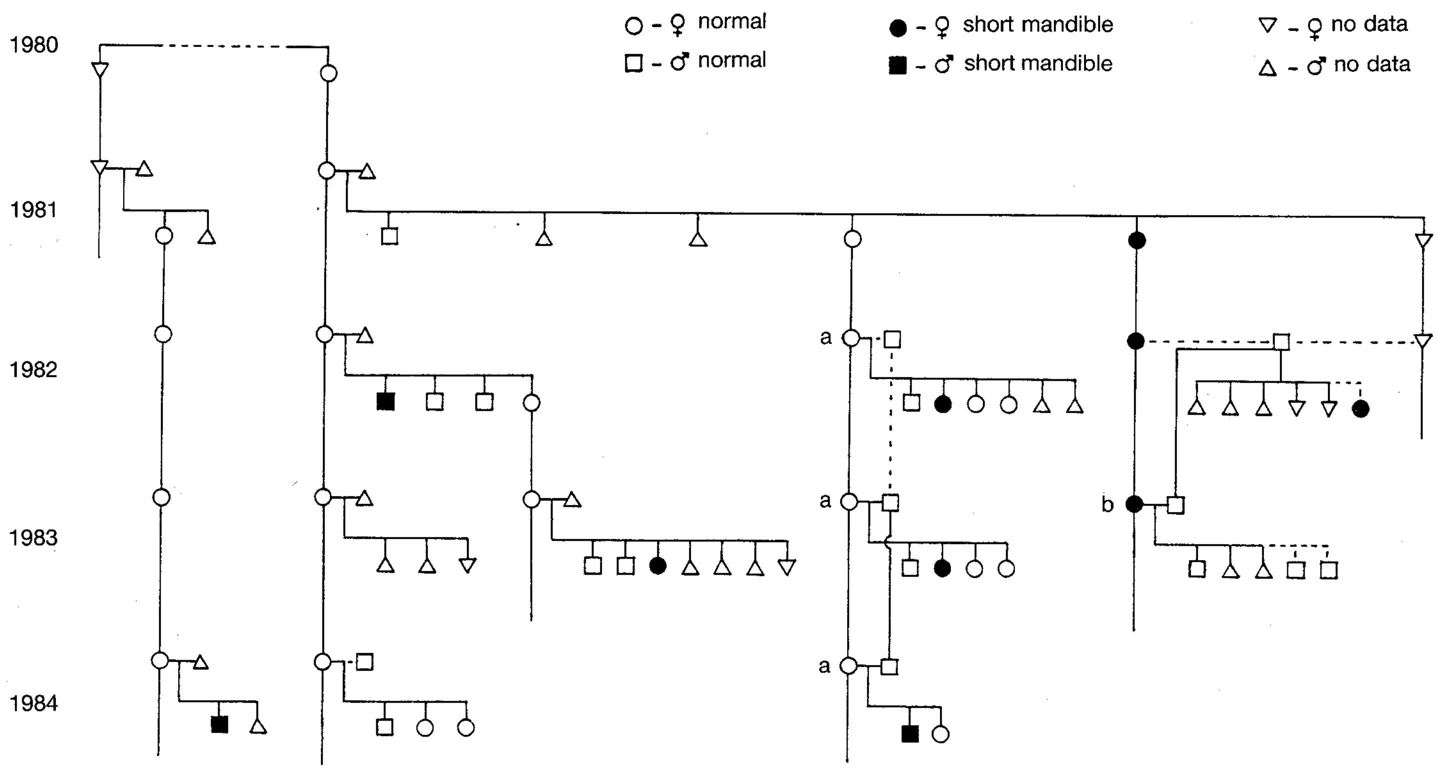

FIG. 4. Diagram of the family relations between normal and aberrant foxes, as far as known from the field research, from 1980 to 1984. Dashed lines indicate uncertain relations. 'a' and 'b' are matings referred to in the text.

Fig. 4. The interesting data in this Figure are the three consecutive litters of the normal female, indicated with 'a', which at least during two years was mated with a normal male. Furthermore, it is noteworthy that at least one of the cubs from the mating, indicated with 'b', of an abnormal female with a normal male showed a normal occlusion.

Discussion

Missing teeth

As already noted by van Bree & Sinkeldam (1969), it is difficult to judge whether absent teeth were originally missing or were lost during life. In several of the skulls we noticed that after the loss of a tooth its socket was to a greater or lesser extent filled with bone tissue. This process of bone growth makes the establishment of missing teeth in older foxes' skulls difficult: the socket of a tooth long lost may have disappeared. A study of missing teeth in foxes should probably be limited to foxes up to the age of two years old, in order to avoid a flaw.

Our data on missing teeth are similar to those obtained by van Bree & Sinkeldam (1969); in a sample of 293 skulls from western continental Europe they found that in 6·5%, 3·1% and 10·9% of the skulls one or two of the P_1, P_2 and M_3, respectively, were absent. Rantanen & Pulliainen (1970) studied 75 fox skulls from eastern Lapland, and found somewhat lower figures: 1·4% of the P_1 and 6·0% of the M_3 were missing, as well as 0·7% of the P_4. Van Bree & Sinkeldam (1969) suggest that there is an evolutionary trend in the red fox towards a reduction of the dentition. Although the mandibles of abnormal skulls in our material have much less room for the premolars than the mandibles of normal skulls, they do not show a higher rate of reduction in number of premolars.

Causal background of the anomaly

The frequency of fox skulls with shortened mandibles in the material from the NHD is unusually high. Among several thousand foxes from England such an anomaly was found only a couple of times (Dr S. Harris, pers. comm.); Dr J. Englund (pers. comm.) could not remember having seen any case of shortened mandibles in several thousand fox skulls from Sweden. *(1) Van Bree & Sinkeldam (1969) found only one skull with a protrusion of the rostrum over the mandibles, among the 293 fox skulls they studied. This skull, belonging to a vixen from the east of the Netherlands, seemed to be similar to the abnormal skulls in our material: both lower canines were piercing the palate, and the Mand/Cbl ratio was low, 0·735. Closer inspection revealed, however, that the mandibles were shortened in the region behind the last molars, instead of in the muzzle region. The difference between upper and lower muzzle length was only 0·50 mm in this skull (see Table I), and the occlusion was abnormal over the whole length of the row of teeth; as a result half of the M_2 as well as the M_3 did not have opposing teeth in the upper jaw. *(2) The left and right side of the two aberrant skulls from eastern Holland were completely alike, as in the abnormal skulls in our material, suggesting a genetical background for both types of shortened mandibles rather than a disease or injury.

Yet another fox skull with apparently shortened mandibles, from the eastern part of the Netherlands, has been reported by a taxidermist (Bos, 1983). Unfortunately no further details are available.

A genetical background of the anomaly is also indicated by the fact that in each of three consecutive litters of the same pair of foxes at least one cub had shortened mandibles (Fig. 4, 'a').

* Notes: (1) and (2) see p. 136

Furthermore, if the cause of the anomaly was an environmental factor we should have expected a gradual transition from normal to short mandible, instead of the clear bimodal distribution in mandible length (Fig. 3). Colyer (1936), Lundström (1960) and Ritter (1937) have already noted the importance of genetic factors in the causation of jaw-related malocclusions.

The bimodal distribution in Fig. 3, showing no intermediate skulls, suggests monogenetic control of the anomaly. In this case the genes responsible for the anomaly must be of recessive nature, as can be deduced from Fig. 4. Crosses between foxes with normal occlusions ('a') resulted in offspring in which at least one of the cubs showed the anomaly. Consequently the parental foxes must both have been heterozygotes, having a dominant gene for normal mandible length and a recessive gene for shortened mandibles.

Schulze & Wiese (1965) studied similar malocclusions in humans and found a great variation in the expression of the anomaly. This observation led them to the conclusion that the anomaly is coded by a number of genes or gene-pairs, instead of by a single gene. The variation in the expression of the anomaly in our material, however, is small and must be due to varying circumstances during growth of the jaws. Solow (1980) emphasized the importance of the interdigitation of upper and lower teeth in the development of the jaws in man. We, however, could not detect such an influence of the occlusion in the development of the abnormal mandibles. Lundström (1960) showed that apart from the way in which the position of the teeth during growth in humans may influence the expression of genetic factors, the quantity of growth hormone and the size of the tongue may also affect the development of the mandible or maxilla.

Underdevelopment of mandibles has been proved to occur as a side-effect of some diseases, at least in man. Oculo-auriculo vertebral dysplasia (Gorlin *et al.*, 1963) and suppurative otitis media (Lundström, 1960) are two of these diseases, both affecting the ear, leading to deafness. It is unlikely that the malocclusion in our material is caused by such an illness, because of the lack of variation in the expression of the anomaly and because some of the anomalous foxes were at least two years old: it is not to be expected that foxes with such a disease will live beyond a few months.

Explanation for the high incidence of the anomaly

Although our sample cannot be assumed to be representative for the living fox population (see below), the incidence of this type of malocclusion in the population is clearly high. This must be the result of a founder effect (Mayr, 1971). The founder effect implies that a population of animals which has arisen in a (more or less isolated) area formerly not occupied by the species usually has originated from only a few so-called founders. This results in the variation in the genetic make-up of the resulting population being much more restricted than the variation present in the gene pool of the main population. The degree of isolation of the area (i.e. the number of subsequent immigrants) and the number of original founders determine the degree of inbreeding which will occur. In the case of the North Holland Dune Reserve, one of the initial few founders of the fox population must have been a bearer of a rare recessive gene for shortened mandibles. Inbreeding and lack of other immigrants into the rather isolated area resulted in the occurrence of homozygotes, in which the anomaly came to expression. Judging from the high frequency of the anomaly, the original gene pool, and thus the number of founders, must have been very small, presumably just one breeding pair. A restricted genetical variation is also suggested by the lack of coat colour variation which has been observed in this population compared to others (J. L. Mulder, pers. comm.).

Two possible disadvantages for foxes with the anomaly have already been mentioned: broken and backwards-curved canines may diminish their grip on rabbits, the main prey in the dune area (Mulder, 1985*b*), and the lower canines often pierce the palate, causing physical inconvenience. A third possible drawback may be that females, giving birth, may have difficulty in removing the amnion and chorion membranes of their cubs, because they cannot use their incisors properly (Naaktgeboren & Ridder, 1975). However, one female with shortened mandibles successfully raised cubs (Fig. 4, 'b').

It is unlikely that natural selection will favour foxes with the anomaly. During the rapid population growth, until stabilization around 1982, the selective forces against the anomaly will have been weak. The majority of the skulls were collected between 1982 and 1985, and the high proportion of skulls showing the aberration may be either a reflection of a high frequency of the anomaly in the population, as a result of the weak selective forces, or on the contrary the result of the selection itself: the anomalous foxes may, driven by hunger, have been more prone to accept the suspect baits provided by poachers, thus entering our skull sample.

In the long run we expect that the frequency of the anomaly in the population will be less, as a result of stronger selective forces in the stable population. It will, however, always be present in some degree, because the majority of the bearers of the recessive gene for shortened mandibles will be heterozygotes, and hence will not be selected against.

We should like to thank the following people for their various contributions during the accomplishment of this paper: the staff of the Waterworks of the Province of North Holland for their help in collecting the fox skulls; A. Rol for his labour in the preparation of the skulls, and the other staff members of the ITZ for their assistance in other respects; Dr R. B. Kuitert (Department of Orthodontics, Free University of Amsterdam), Dr A. J. Klarenberg (Department of Population and Evolutionary Biology, University of Utrecht) and F. P. G. Princée (Dutch Federation of Zoological Gardens) for their suggestions on the causal background of the anomaly; A. Christoffels, E. S. M. Hagelen, A. J. Klarenberg, E. Koet and P. Twisk for the loan of the fox skulls in their possession; and an unknown referee for his valuable remarks on earlier drafts of the manuscript. Dr S. Harris from Bristol University was so kind as to correct the English.

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Notes: Added in proof

(1) H. Ansorge (pers. comm.) found that 0·5% of about 700 fox skulls from Eastern Germany (GDR) had shortened mandibles.

(2) Among 208 fox skulls collected by the Research Institute for Nature Management (Arnhem) in eastern parts of the Netherlands, a further two skulls with a clear difference between upper and lower jaw were discovered. One of these was very similar to the skull described above, i.e. showing a shortening of the mandible in the region behind the molars, with a Mand/Cb1 ratio of 0·715 and a difference between upper and lower muzzle length of 2·70 mm. The other aberrant skull in this collection most probably was not a case of shortened mandibles, but of an elongated rostrum. Unfortunately, the condylobasal length could not be measured because of damage, but the rostrum had extra P^1s on both sides and still plenty of room between the teeth.