

Increase of skull size in the red fox (*Vulpes vulpes*) and Eurasian badger (*Meles meles*) in Denmark during the twentieth century: an effect of improved diet?

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ABSTRACT

The skulls of 272 red foxes (*Vulpes vulpes*) and 308 Eurasian badgers (*Meles meles*) collected in Denmark over the last 120 years were measured to determine any temporal changes in skull size (and, by implication, body size) during the studied period. We wished to determine whether global warming had resulted in a decrease in skull and body size in accordance with Bergmann's rule. Contrary to our predictions, there were no significant negative relationships between any of the four skull characters measured and mean annual temperature. Among badgers, two of the four characters measured had increased significantly during the twentieth century (zygomatic breadth by about 2% and length of upper molar by about 3.5%), but only in Jutland. In the red fox, three of the four skull characters measured had increased significantly during the twentieth century (zygomatic breadth by about 5%, length of fourth upper premolar by about 7% and diameter of canine by about 9%), with one parameter (zygomatic breadth) increasing twice as fast in Zealand as in Jutland. All the above three characters are closely associated with diet: the size of the zygomatic arch is closely related to the size of the masseter muscle, the size of the carnassial and the diameter of canine are generally associated with prey size, and the size of the first molar is associated with grinding of grain and larger invertebrates. Larger teeth enable a predator to take and handle larger prey items. However, the fourth parameter (greatest length of skull) had not increased during the studied period. Since all the above skull characters are significantly related to body size, these results indicate that the body size of both species had increased during the twentieth century. The increase in skull characters is probably related to contemporaneous changes in Danish agriculture and land use, which, in turn, resulted in changes to the foxes' and badgers' diets.

Keywords: body size, Denmark, diet, Eurasian badger, red fox.

INTRODUCTION

Adult body size may vary geographically and over time and is influenced by several factors, including nutrition and ambient temperature. In many birds and mammals, conditions experienced during early development affect growth and, ultimately, body size (Ulijaszek

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et al., 1998; Henry and Ulijaszek, 1996). Adult body size appears to be a function of the length of time in which the growing individual has unhindered access to high-quality food (Geist, 1987). This is exemplified by observations that during the last two centuries body height and weight in humans have increased significantly (secular trend), predominantly in European and European-origin populations (Ulijaszek *et al.*, 1998). The prime determinants of this trend are considered to be improved nutrition and the availability of public health services (Ulijaszek *et al.*, 1998).

Bergmann's rule states that in 'warm blooded animals, races from warm regions are smaller than races from cold regions' and it is probably the best known rule in zoogeography (Mayr, 1970). Bergmann's rule was interpreted as an adaptation to ambient temperature: the larger body surface area relative to volume of the smaller races serves as an efficient heat dissipator in warm climates, whereas the small body surface area relative to volume may help in heat conservation in cold climates. Global mean surface temperatures have increased by 0.6°C since the late nineteenth century (IPCC, 1995), and mean annual temperature in Denmark increased by about 1°C during the twentieth century (Cappelen, 2002). Recently, it has been claimed that global warming has affected body size in several species of passerines (Yom-Tov, 2001) and in a rodent (Smith *et al.*, 1998). Although none of these studies represents a controlled experiment, these trends are explained most parsimoniously by a correlation with recent climatic change (Hughes, 2000).

In homeothermic animals, a change in skull size and body mass can occur rather rapidly, as reported for animals introduced into new environments. For example, within 100 years of its introduction to North America and New Zealand, the body size of the house sparrow, *Passer domesticus*, correlated positively with seasonality and annual temperature range in both regions (Selander and Johnston, 1967; Johnston and Selander, 1971; Baker, 1980; Lowther and Cink, 1992). Similarly, within 50 years of its introduction to New Zealand, the body size of the brushtail possum, *Trichosurus vulpecula*, correlated with ambient temperature as it does in Australia from where it was introduced (Yom-Tov *et al.*, 1986).

Denmark consists of a peninsula (Jutland) and many islands, the largest of which are Zealand (where Denmark's capital, Copenhagen, is located) and Funen. The red fox (*Vulpes vulpes*) is a common carnivore throughout the country. Since 1955, the annual number of red foxes shot per county has been recorded (Jensen, 1977; Strandgaard and Asferg, 1980; Madsen *et al.*, 1996). Using these data, Forchhammer and Asferg (2000) have shown that there was no significant difference in the annual number of foxes bagged and the number of foxes shot per unit hunting effort. Several authors (Forchhammer *et al.*, 1998; Cattadori *et al.*, 1999) have shown that hunting statistics provide a good estimate of actual population abundance, thus the above probably reflects true population trends. In Jutland in 1984, foxes were found with sacroptic mange and the disease spread quickly throughout the peninsula, as well as to the island of Bornholm (but not in Zealand), followed by a dramatic decline in fox densities in these areas (Forchhammer and Asferg, 2000).

In Denmark, the red fox is a generalist predator, preying upon rodents, partridges (*Perdix perdix*), pheasants (*Phasianus colchicus*), brown hares (*Lepus europaeus*) and roe deer fawns (*Capreolus capreolus*) (Jensen and Sequeira, 1978). Laursen (2002) found that rural foxes feed mainly on voles (*Microtus*), but also on mice (*Apodemus*) and other rodents, followed by birds and, to a lesser extent, fruit and invertebrates, while urban foxes supplement this diet with discarded human refuse. Changes in land use and agricultural practices in Denmark during the second half of the twentieth century were followed by an increase in the number of pheasants bred for release into the countryside, as well as an increase in the

number of roe deer (Olesen *et al.*, 2002). Danish game statistics indicate that the annual bag of pheasants increased linearly from about 300,000 in the 1940s to about 750,000 in the 1990s, while the annual bag of roe deer increased from about 15,000 to about 100,000 during the same period (<http://www.dmu.dk>). Roe deer fawns and pheasants have rarely been found in the stomachs of adult foxes (Laursen, 2002). Negligible as food items most of the year, these two prey species may nevertheless be of crucial importance for the growth of cubs.

The Eurasian badger (*Meles meles*) is a common predator throughout Denmark. After the last ice age it spread throughout the country, but then disappeared from Zealand about 8000 years ago. However, around the middle of the nineteenth century it was re-introduced to the islands of Lolland, Falster and Zealand where it quickly became common (Aaris-Sørensen, 1980; Asferg, 1991). The badger is an omnivorous and opportunistic forager, feeding on earthworms and other invertebrates, birds' eggs and chicks, rodents and carrion, including road kills, as well as on fruits, bulbs, acorns, oats and wheat (Andersen, 1954; Asferg, 1991; Macdonald and Barrett, 1993).

In this article, we examine two conflicting hypotheses: (1) global warming has had a negative effect on the skull size (and, by implication, body size) of Danish red foxes and Eurasian badgers, as expected from Bergmann's rule; (2) increased food availability has a positive effect on skull size.

The size of food-related characters such as teeth and some skull muscles is associated with diet composition, and the skull characters of sympatric competitors may be influenced by interspecific competition (Dayan *et al.*, 1989). As indicated above, there is some overlap in the composition of the diet of the fox and the badger, and such overlap may result in interspecific competition. Thus, we also examined the possibility that the two species compete by comparing the size of their food-related characters.

MATERIALS AND METHODS

The skulls of 272 red foxes and 308 Eurasian badgers were measured at the Zoological Museum of Copenhagen (ZMUC); foxes' skulls were also measured at the Aarhus Natural History Museum. Most of the museum specimens had been either hunted or gathered as road kills, and were collected during the period 1862–2000. For each skull we noted (from its label or museum catalogue) its sex, locality and date of collection, and when available also body weight and body and tail length. Using digital calipers, four measurements were taken from each skull to an accuracy of 0.01 mm: greatest length, zygomatic breadth, the length of the largest upper cheek teeth – the shearing upper premolar (carnassial) in the fox and grinding upper molar in the badger – and diameter of the canine. All of these characters are closely associated with diet. The greatest length is associated with the size of the temporal muscles, which are important to overcome the resistance of prey to occlusion, and the zygomatic arch is closely related to the size of the masseter muscle, which pulls the jaw forward and upward; both muscles are important in chewing. The size of the canine is generally associated with prey size (Ewer, 1973). Larger canines enable a predator to take and handle larger prey items, while larger premolars and molars enable it to crush larger prey effectively, or to grind grain and other hard food items (Romer, 1962). In fact, canids kill their larger prey by several slashing bites (Ewer, 1973; Leyhausen, 1979), while small prey are killed by breaking the neck during vigorous head-shaking movements or by crushing (Sietz, 1950; Leyhausen, 1965).

A preliminary test indicated that young specimens differed significantly from adults in all four characters; hence no juvenile was included in further analysis. Adults were defined as such by the lack of juvenile teeth and the fusion of the cranium bones.

Denmark consists of a peninsula (Jutland) and many islands, the largest of which are Zealand and Funen. Several islands (i.e. Lolland, Falster and Møn) lie close to Zealand. Each specimen was allocated either to Jutland, Funen or Zealand and its adjacent islands. Most of our specimens were from Jutland and Zealand and only very few specimens were from other islands. A recent study (Simonsen *et al.*, 2003) has shown that foxes from the Copenhagen area differ from those of rural Zealand and Jutland in five skull ratios. Accordingly, each fox specimen was also allocated either to rural Jutland (no specimens came from urban Jutland), urban Zealand or rural Zealand. Urban foxes were defined as those collected in Copenhagen or adjacent towns with little access to voles (*Microtus agrestis*, *Clethrionomys glareolus* or *Arvicola terrestris*) or mice (*Apodemus* spp.).

Climatological data were taken from Cappelen (2002).

Statistical analysis

To determine whether skull size of the red fox and Eurasian badger had undergone change during the studied period, we performed multiple regression tests, with year of collection, sex (dummy variable) and region (dummy variable) as independent variables and greatest length of the skull, zygomatic breadth, length of the upper premolar/molar and diameter of the canine as dependent variables. Two sets of tests were run for each variable: one between urban and rural Zealand and one between rural Zealand and rural Jutland.

RESULTS

Red fox

The results indicated that zygomatic breadth, length of the fourth upper premolar and diameter of the canine, but not greatest length of the skull, had increased significantly in the red fox during the studied period in both Jutland and rural Zealand (Table 1). In Zealand, the calculated rate of increase between 1900 and 2000 for males and females was 4.6 and 4.8% respectively for zygomatic breadth, 6.9 and 7.2% respectively for length of upper premolar, and 8.7 and 9.5% respectively for diameter of the canine. The rate of increase in zygomatic breadth was twice as great in Zealand as in Jutland (males: 4.7 and 2.3% in Zealand and Jutland respectively; females: 4.9 and 2.4% in Zealand and Jutland respectively). Zygomatic breadth, length of the upper premolar and diameter of the canine, but not greatest length of the skull, had increased significantly during the studied period and at a similar rate in both rural and urban Zealand (Table 2). In both male and female Zealand foxes, the greatest length of the skull of rural foxes was slightly but significantly larger than that of urban foxes (Table 2). All of the above skull characters were larger in males than females (Tables 1, 2). The temporal increase in zygomatic breadth for the sample as a whole is shown in Fig. 1.

There were significant relationships between all the skull characters and body weight, body length and tail length (Table 3), indicating that all four skull characters are good estimators of adult body size in foxes.

Table 1. Danish fox skull measurements for Zealand and Jutland rural samples: coefficients and significance of multiple regression models of the relationships between four skull characters and year of collection (1900–2000), sex (male and female) and region (Zealand and Jutland)

Predicted variable	<i>n</i>	R_{adj}^2 (%)	Year	Sex	Region	Year × region
Greatest length of skull	195	41.9	n.s.	−8.4 <i>P</i> < 0.001	n.s.	n.s.
Zygomatic breadth	195	34.9	0.0385 <i>P</i> < 0.001	−4.22 <i>P</i> < 0.001	n.s.	−0.01968 <i>P</i> < 0.008
Fourth upper premolar length	195	24.3	0.00778 <i>P</i> < 0.001	−0.67 <i>P</i> < 0.001	n.s.	n.s.
Diameter of canine	193	26.0	0.0046 <i>P</i> < 0.001	−0.595 <i>P</i> < 0.001	n.s.	n.s.

Note: In both regions, zygomatic breadth, length of fourth upper premolar and diameter of canine increased significantly during the study period. The rate of increase in zygomatic breadth was twice as great in Zealand as in Jutland. All characters were larger in males than females. Non-significant interactions are not presented.

Table 2. Danish fox skull measurements for Zealand rural and urban samples: coefficients and significance of multiple regression models of the relationships between four skull characters and year of collection (1900–2000), sex (male and female) and region (rural and urban)

Predicted variable	<i>n</i>	R_{adj}^2 (%)	Year	Sex	Region
Greatest length of skull	145	33.8	n.s.	−7.737 <i>P</i> < 0.001	−1.907 <i>P</i> < 0.03
Zygomatic breadth	145	42.0	0.0378 <i>P</i> < 0.001	−4.743 <i>P</i> < 0.001	n.s.
Fourth upper premolar length	145	25.9	0.01014 <i>P</i> < 0.001	−0.503 <i>P</i> < 0.001	n.s.
Diameter of canine	143	29.2	0.06123 <i>P</i> < 0.001	−0.587 <i>P</i> < 0.001	n.s.

Note: In both regions, zygomatic breadth, length of fourth upper premolar and diameter of canine increased significantly during the study period. Greatest length of the skull of rural foxes was slightly but significantly larger than that of urban foxes. All characters were larger in males than females. Non-significant interactions are not presented.

Mean annual temperature in Denmark increased during the twentieth century (Fig. 2). However, no significant relationships were found between three of the four skull characters and mean annual temperature at the year of collection (greatest length of the skull: $F = 0.167$, $P = 0.6831$; zygomatic breadth: $F = 0.683$, $P = 0.4092$; diameter of the canine: $F = 3.787$, $P = 0.0527$), whereas length of the upper premolar increased significantly in relation to temperature ($F = 8.763$, $P = 0.0034$), contrary to the prediction of Bergmann's rule.

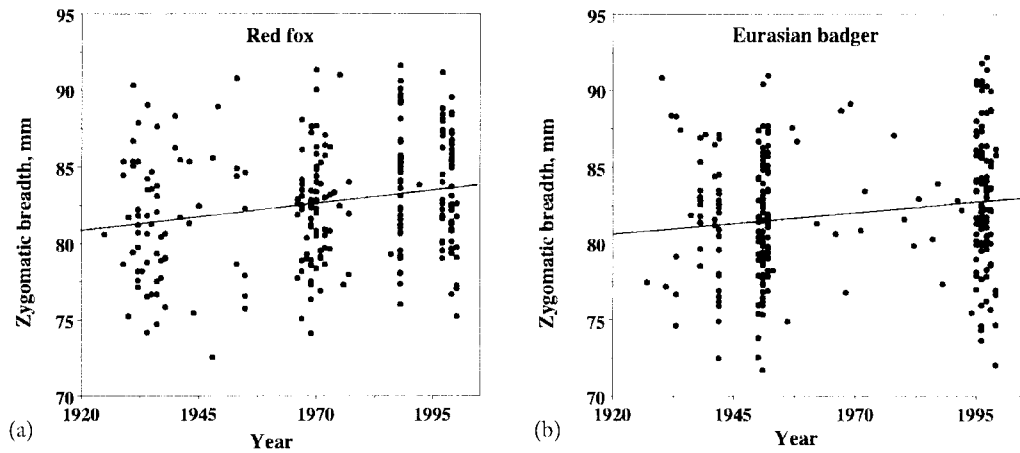


Fig. 1. The relationship between year of collection and zygomatic breadth in (a) the red fox ($F = 13.40$, $P < 0.0003$) and (b) the Eurasian badger ($F = 6.08$, $P = 0.0143$).

Table 3. The relationships between four skull and three body characters of the red fox in Denmark

Character		Body weight ($n = 35$)	Body length ($n = 49$)	Tail length ($n = 45$)
Greatest length of skull	R^2	0.591	0.481	0.405
	P	< 0.0001	< 0.0001	< 0.0001
	n	35	50	46
Zygomatic breadth	R^2	0.670	0.359	0.284
	P	< 0.0001	< 0.0001	< 0.0001
	n	35	50	46
Fourth upper premolar length	R^2	0.439	0.205	0.256
	P	< 0.0001	0.001	0.0003
	n	33	48	46
Diameter of canine	R^2	0.208	0.168	0.148
	P	0.0077	0.0038	0.01

Eurasian badger

The results indicated that zygomatic breadth and length of the upper molar, but not greatest length of the skull and diameter of the canine, had increased significantly in badgers in Jutland but not in Zealand (Table 4). In Jutland, the calculated rate of increase between 1900 and 2000 for males and females was 2.0 and 2.1% respectively for zygomatic breadth and 3.5 and 3.6% respectively for length of the upper molar. All of the above skull characters were larger in males than females (Table 4). The temporal increase in zygomatic breadth for the sample as a whole is shown in Fig. 1.

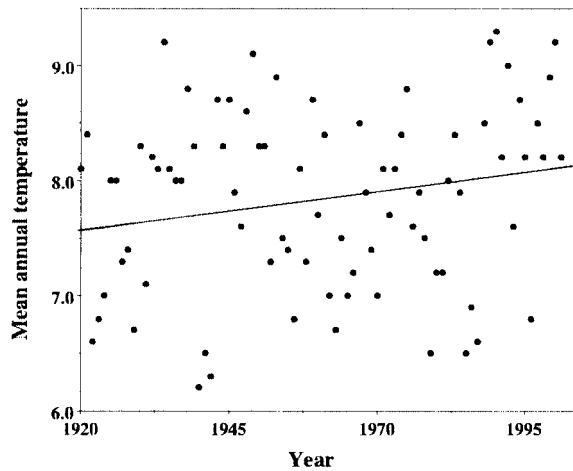


Fig. 2. Mean annual temperatures in Denmark, 1920–2000.

Table 4. Danish badger skull measurements: coefficients and significance of multiple regression models of the relationships between four skull characters and year of collection (1900–2000), sex (male and female) and region (Zealand and Jutland)

Predicted variable	<i>n</i>	R^2_{adj} (%)	Year	Sex	Region	Year \times region
Greatest length of skull	268	21.7	N.S.	-4.453 $P < 0.001$	N.S.	N.S.
Zygomatic breadth	274	34.9	N.S.	-5.047 $P < 0.001$	N.S.	0.0168 $P = 0.002$
Upper molar length	275	11.4	N.S.	-0.431 $P < 0.001$	N.S.	0.00515 $P < 0.001$
Diameter of canine	280	44.9	N.S.	-0.827 $P < 0.001$	-0.144 $P = 0.016$	N.S.

Note: The zygomatic breadth and length of upper molar increased significantly during the study period in Jutland, but not in Zealand. Diameter of the canine was significantly larger in Zealand than in Jutland. All characters were larger in males than females. Non-significant interactions are not presented.

There were significant relationships between three of the four skull characters and body weight (greatest length of the skull: $n = 80$, $R^2 = 0.262$, $P < 0.0001$; zygomatic breadth: $n = 85$, $R^2 = 0.244$, $P < 0.0001$; diameter of the canine: $n = 88$, $R^2 = 0.226$, $P < 0.0001$). Diameter of the canine was significantly greater in Zealand than in Jutland. No significant relationship was found between body weight and length of the upper molar ($n = 85$, N.S.). There were insufficient data to examine possible relationships between the four skull characters and other body measures, such as body, tail, ear and hindfoot lengths.

There were no significant relationships between any of the four skull characters and mean annual temperature at the year of collection (greatest length of the skull: $F = 0.002$,

$P = 0.9613$; zygomatic breadth: $F = 0.192$, $P = 0.6615$; length of the upper molar: $F = 1.709$, $P = 0.1927$; diameter of the canine: $F = 2.578$, $P = 0.1101$).

Comparison of the skull characters of the two species

In Denmark, there was no significant difference in zygomatic breadth between badgers and foxes (males: mean of 84.50 and 84.31 mm for badgers and foxes respectively; females: mean of 79.56 and 79.72 mm for badgers and foxes respectively) or in length of the largest grinding teeth in females (mean of 14.63 and 14.70 mm for badgers and foxes respectively). Foxes had a greater length of the skull than badgers (males: mean of 154.16 and 140.16 mm for badgers and foxes respectively, $t_{291} = 23.7$, $P < 0.0001$; females: mean of 146.34 and 135.73 mm for badgers and foxes respectively, $t_{249} = 20.4$, $P < 0.0001$). Male foxes had longer largest grinding teeth than male badgers (mean length of upper premolar in foxes *vs* mean length of the upper molar in badgers: 15.33 *vs* 15.01 mm, $t_{298} = 3.5$, $P = 0.0005$). Also, the diameter of the canine was greater in badgers than foxes (males: mean of 8.56 and 7.38 mm for badgers and foxes respectively, $t_{298} = 18.8$, $P < 0.001$; females: mean of 7.71 and 6.77 mm for badgers and foxes respectively, $t_{251} = 15.3$, $P < 0.0001$).

DISCUSSION

Our results show that of the four skull characters measured in the fox, three (zygomatic breadth, length of fourth upper premolar and diameter of canine) increased significantly during the twentieth century, with one parameter (zygomatic breadth) increasing faster in Zealand than in Jutland. Among the badgers, two characters (zygomatic breadth and length of upper molar) increased significantly in Jutland, but not in Zealand. There were no significant negative relationships between the size of the skull characters and mean annual temperature. Thus, the hypothesis that global warming would result in a decrease in skull and body size as predicted by Bergmann's rule is rejected. Zygomatic breadth, length of the largest grinding teeth and diameter of the canine are closely associated with diet, and the importance of the carnassials to canids in killing and cutting prey, and of large grinding teeth to badgers, is clear. Hence, the observed increase in size of the above characters indicates that an improved diet affected the size of the badger and the fox in Denmark. However, greatest length of the skull did not increase during the studied period. Since zygomatic breadth, length of the largest grinding teeth and diameter of the canine are significantly related to body size (although only zygomatic breadth and length of the upper molar increased in the badger), our findings, particularly the increase in zygomatic breadth and length of the fourth upper premolar, which were highly correlated with body mass ($R^2 = 0.670$ and 0.439 , respectively; Table 3), indicate an increase in body size during the course of the twentieth century.

Similar phenomena have been observed in other animals. For example, in harbour porpoises (*Phocoena phocoena*), increased prey availability (presumably due to a hunting pressure induced decrease in population density) resulted in an increase in body length of calves and earlier sexual maturity of females (Read and Gaskin, 1990). Another example is Yom-Tov's (2003) observation that, in Israel, body length of four species of carnivores commensal with humans increased significantly during the second half of the twentieth century; he attributed this change to improved diet. Hence, it is reasonable to assume

improved diet is a cause of the observed increase in skull and body size of the red fox and Eurasian badger.

We cannot provide a clear-cut explanation for the increase in skull measurements observed in this study, or for the differences noted in the pattern of increase between Jutland and Zealand. Several factors may be related to the observed changes, sometimes acting in contrasting ways, and additional investigations are required before a firm conclusion can be made. However, we would like to point out some factors that may have influenced the above observations. These factors are probably related to an improved diet influencing either the growth of the young animals or the survival and stronger reproductive success of those individuals that can handle larger prey or food items.

Anthropogenic factors are responsible for the appreciable increase in food availability for both predators throughout the last century. The significant rise in human living standards was generally followed by an increase in the amount of garbage and its nutritional quality. Garbage is readily consumed by Danish foxes, mainly in the towns, but also in rural areas (Laursen, 2002). Road kill is another common food source that increased dramatically, as length and width of roads increased as well as the number of cars and their travelling speed. During the second half of the last century, Danish agriculture underwent a major change, with poor agricultural land being left uncultivated and taken over by forest and shrub. This, and better hunting management, were followed by an increase in the number of roe deer in the countryside (Olesen *et al.*, 2002). Throughout Denmark, small farms were merged to create larger ones, and many larger farms and estates, particularly in Zealand and neighbouring islands, increased their income by breeding and releasing pheasants for hunters. Small roe deer fawns and pheasants are among the largest food items consumed by foxes (Jensen and Sequeira, 1978) and, although they are rarely found in the stomachs of adult foxes, they are brought to the dens for consumption by the cubs (Laursen, 2002). Only very young fawns are probably taken, and incubating pheasants are more easily taken while on the nest. Although we do not have exact figures for the proportion of these two prey items in the diet of foxes, it is probably safe to say that over the years and corresponding with the increase in game bag figures, there has also been an increase in the number of available pheasants and roe deer, more so in Zealand than in Jutland. We cautiously suggest that the increase in zygomatic breadth (with the associated increase in size of the masseter muscle), premolar and canine teeth may indicate that foxes are now consuming larger food items than before. The fact that the above characters increased at a faster rate in Zealand (where more pheasant are available in the countryside) than in Jutland supports this conclusion. On the other hand, the fact that roe deer fawns and incubating pheasants are available for only a very short period of the year may indicate that this source of nutrition is of minor importance in determining skull size.

Changes in agricultural production and management of the landscape have caused alterations in the badger diet in Denmark. Oat and wheat are highly preferred to barley by badgers when they forage on cereals (Kruuk, 1989). The total amount of cereals produced increased 2.64-fold, and the total annual amount of oat and wheat increased 4.56-fold, between 1953 and 1998 (*Statistical Yearbook*, 1954, 1999). Madsen *et al.* (2002) studied the diet of the badger in Jutland between 1995 and 1998, compared it with the diet of this species during the 1950s (Andersen, 1954), and showed that the importance of cereals as food during the summer had decreased in comparison to the 1950s (Andersen, 1954), while the importance of mammals (rodents) as prey items in summer had increased during this period. Hence, the amount of cereals produced probably had no direct effect on skull

characters. However, the increase in the amount of cereal produced may have influenced the number of rodents available as prey.

The temporal increase in skull characters was not uniform in Denmark. Among foxes, the rate of increase in zygomatic breadth was twice as great in Zealand as in Jutland, and among badgers zygomatic breadth and length of the upper molar increased only in Jutland. This increase in skull characters in one species in one area thus appears to be associated with the lack of increase in the other. Although the fox and the badger belong to two different families and feeding guilds, the above facts raise the possibility that there are interactions between the two species. This assumption may be supported by the fact that there was no significant difference in zygomatic breadth between foxes and badgers and in length of the largest shearing or grinding teeth in males (premolar in foxes, molar in badgers), and their body weights were also similar (Jensen, 1993). We suggest that the fox is better equipped to take advantage of the increase in anthropogenic food availability, as indicated by the fact that the rate of increase in skull characters in foxes is greater than that in badgers. This is especially true since foxes can hunt the pheasants and young deer fawns that are more readily available in Zealand, hence its increase mainly in this area. Competition with the fox in Zealand may have prevented the badger from increasing there, whereas it was able to take advantage of the increase of food availability in Jutland. This hypothesis can be tested in the future by a detailed study of the diet of sympatric Danish foxes and badgers.

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