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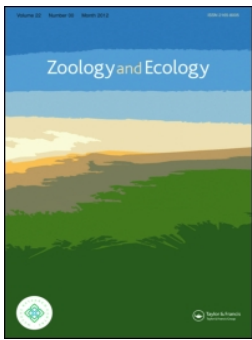
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Variability in body mass and sexual dimorphism in Danish red foxes (*Vulpes vulpes*) in relation to population density

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ABSTRACT

For the first time, temporal variability in body size and sexual dimorphism is revealed in foxes *Vulpes vulpes* from the same geographical area at over time. The weights and lengths of 552 Danish foxes were documented during three different periods: 1965–1977, 2012–2014 and the winter of 2015/2016. During the first and the third periods, the fox population was below the carrying capacity due to hunting pressure and canine distemper, respectively. Adult males were significantly ($p < 0.01$) heavier (mean weight: 7.7 kg and 7.5 kg respectively) in periods of low population density, i.e. 1965–1977 and compared to 2015/2016, compared to 2012–2014, when population density was high (the mean weight: 6.8 kg). However, no significant differences were found in the weight of females. Hence, sexual dimorphism ranged from 7.6 to 3.6 in adult foxes in low and high-density periods, respectively. During the winters of 2012–2014, no difference in body fat measured by rump fat thickness (RFT) was found between age groups and genders in contrast to 2015/2016, when RFT was significantly ($p < 0.001$) larger in adult females (mean RFT: 0.77 cm) than in adult males (mean RFT = 0.58 cm).

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Body size; body weight; fat; mating strategies; mating behaviour; fox; population structure

Introduction

The size and weight of red foxes *Vulpes vulpes* vary significantly across different regions of the world. The mean body mass of adult red fox males ranges from 4.3 to 7.6 kg and that of females from 3.6 to 6.5 kg. The body length of males varies between 96 and 115 cm, and that of females between 91 and 110 cm (Cavallini 1995; Lloyd 1980). Males are generally larger and heavier than females, and the average dimorphism is between 4.4 and 7.7% (Cavallini 1995). North American red foxes have a relatively light body weight for their length, and exhibit a high degree of sexual dimorphism. British foxes, in contrast, are among the heaviest foxes in the world with a relatively low degree of sexual dimorphism (Cavallini 1995; Lloyd 1980). The size of foxes also varies on a smaller, regional scale. For example, foxes recorded in Scotland were found to be heavier than those in England, and Welsh foxes were found to be the lightest (Lloyd 1980). Foxes may also vary in size over time. Skull measurements of red foxes in Denmark showed that during the 20th century foxes had increased in size (Yom-Tov, Yom-Tov, and Baagøe 2003). Variation in body size has also been recorded in areas where the abundance of rodents fluctuates widely (Englund 2006; Lindström 1983).

The mean weights of Danish foxes previously given in the literature were 7.6 kg ($n = 252$) for males and 6.1 kg ($n = 198$) for females, with the recorded maximum weight of 12.3 kg and maximum length of 165 cm (Bavnsgaard 1983; Lloyd 1980). However, during the investigation into the diet of Danish foxes in 2012–2014, the lower mean weight of 6.6 kg ($n = 77$) was discovered for males, and 5.8 kg ($n = 80$) for females (Pagh et al. 2015).

A British study into foxes showed that the weather-mediated availability of food for cubs was a key developmental factor for juveniles, which subsequently affected their body mass as adults (Soulsbury et al. 2008). A positive correlation was found between the full-grown body mass of foxes and the inter-annual variation in total rainfall during July, which was also found to be positively correlated to the proportion of earthworms in the diet of cubs (Soulsbury et al. 2008). Easily accessible food items such as earthworms at a key developmental stage may affect the full-grown mass of foxes (Soulsbury et al. 2008). However, many species can compensate for periods of nutritional restrictions and slow growth early in life by growing faster at other times, at least before maturity (Crisuolo et al. 2008; Lindström 1983; Ryan 1990). In a study conducted in Spain, the foxes living in highly productive habitats were found to be larger than those

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living in less productive habitats (Gortazar, Travaini, and Delibes 2000).

Bergmann's rule predicts that warm-blooded animal sub-species are smaller in warmer regions than in cold regions (Mayr 1970). Although supported by some studies (Cavallini 1995; Dayan et al. 1989; Kolb and Hewson 1974), this rule has not been confirmed in all cases. In a study of Spanish foxes, the latitude explained only a minor percentage of the variation in skull size, a measurement that is correlated with the body size (Yom-Tov et al. 2007).

With regard to carnivores, little support has been found for the island rule, which predicts a negative correlation between the relative abundance of island individuals and their body mass (Meiri, Dayan, and Simberloff 2004). However, a 10% increase in the inbreeding coefficient might result in a 10% reduction in traits closely associated with fitness, such as longevity, fecundity and body size (Frankel and Soulé 1981).

It seems that several factors such as climate, latitude, population density, food availability and genetic components can affect the weight and body length of foxes (Cavallini 1995; Gortazar, Travaini, and Delibes 2000; Englund 2006; Lindström 1983; Lloyd 1980; Kolb and Hewson 1974; Meiri, Dayan, and Simberloff 2004; Soulsbury et al. 2008). Currently, very little is known about the underlying mechanisms of fox size on a local scale.

To assess the effect of population density on the size and sexual dimorphism of foxes, we compared the body measurements of three fox samples collected from Denmark over three periods in relation to population density changes induced by different hunting and epidemic (canine distemper) pressures. We expected fox weight to be inversely dependent on density, and as the study area did not vary, we assumed that genetic, geographical and climatic factors would not influence the tested variables. Moreover, we tested for possible regional differences in the body mass of foxes.

Materials and methods

Data collected over three different periods were compared in order to determine whether the body size of foxes in Denmark varied as a function of population density.

Study area

Foxes were collected from agricultural areas in Jutland, the Danish part of the Cimbric Peninsula covering an area of 29,775 km. The northernmost point of Jutland is located at 57°43'N/10°37'E (lat./long.).

The three collections of foxes

Data on the length and weight of foxes for the period 1965–1977 were used alongside the associated 202 fox skeletons (no. 13000 to 13202) kept at the Natural History Museum, Aarhus. Of these, 178 individuals (collection A) had been ear-tagged as cubs or as juveniles in a mark-recapture study by Jensen (1973). Most of the individuals were weighed as cubs and later measured and/or weighed again when returned dead as juveniles or adults. The foxes were mainly from Jutland: 128 from Mid Jutland, 19 from Northern Jutland, 10 from Southern Jutland. In addition, 19 individuals arrived from Zealand and 2 from Bornholm. The majority of the foxes (152) were shot, 12 were found dead, 8 were killed by car or harvester, 3 were killed by dogs and 3 died of other causes. Many of them had been ear-tagged as cubs in April and May, and most (77%) of them were recovered during the hunting season lasting from September to February. In the period 1965–1977, around 30% of the juvenile foxes were recovered dead during their first year mainly due to hunting (Jensen 1973). The birth date of red foxes has not been studied in Denmark, however, when taking latitude into account, we can assume that most cubs were born between mid-March and the 1st of April (Lloyd 1980; Lloyd and Englund 1973). The age of an individual was therefore calculated as the time between the 1st of April in the year when the cub was ear-tagged and the time of death.

The second collection (B) included 187 foxes more than 6 months old collected between June 2012 and September 2014. All these foxes were from Jutland: 143 from Mid Jutland, 44 from Southern Jutland. The majority (126) of them were shot, 25 were killed by car, 28 were trapped and 8 died of other causes. Most of the foxes (95%) were collected during the hunting season from September to February in the winter of 2012/2013. The age of foxes from the collection B was determined by counting incremental annuli in the canine teeth following Roulichová (2007). Foxes that were not too injured, skinned or decomposed were weighed to the nearest 100 g, and a measuring tape was used to determine their body length to the nearest 0.5 cm from the tip of the nose to the last vertebra of the tail. The rump fat thickness (RFT) to the nearest mm of subcutaneous fat around the pelvic girdle was used as a relative measure of the amount of body fat in accordance with Prestrud and Nilssen (1992) and Prestrud and Pond (2003).

The third collection (C) consisted of 187 foxes shot during the hunting season in the winter of 2015/2016. All these foxes were from Jutland: 84 from Mid Jutland, 30 from Northern Jutland, 50 from Southern Jutland and 23 from unknown locations in Jutland. Foxes from this collection were weighed and measured, their age being determined using the same method and by the same individual as in the case of collection B.

Comparing measures and age of foxes from the three collections

The weight of foxes is a well-defined measure, while length may be dependent upon the measuring method. Since the length of foxes from collection A was measured not by the same person that measured collections B and C, we compared the length of foxes only from collections B and C. As the RFT was not available from the museum's collection, we compared only foxes from collections B and C.

Despite some uncertainty, cementum lines are a widely accepted method for determining the age of foxes (Grue and Jensen 1973; Harris 1978). As the first cementum line develops between August and October of the animal's second year of life (Grue and Jensen 1973), the age of the individuals with no cementum lines may theoretically range between 6 months and 1.5 years. However, as most foxes from collections B (95%) and C (100%) were recovered during the hunting season from September to February, most of them were without cementum lines. Thus, their age was presumed to range between 6 and 11 months, and they were grouped as subadults.

By age, the foxes were divided into two groups: subadults (between 6 and 12 months) and adults (over 12 months) in agreement with Harris and Trehwella (1988). In addition, adults were further subdivided into the age groups of: 1, 2 and 3+ years, the latter group being combined due to the relatively small number of foxes surviving over three years. The few foxes with more than three cementum lines were pooled together in order to eliminate the small sample size and any uncertainty in determining the age of foxes over three years (Grue and Jensen 1973; Harris 1978).

National game bag records and demography as a proxy for population density

In Denmark, it is mandatory to report game bags and therefore the National Game Bag Records (NGBR) can

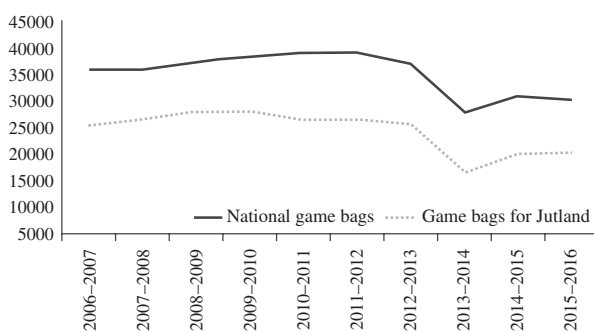


Figure 1. The 2005–2015 National game bag records (solid line) of Danish foxes and the game bags from Jutland (dotted line). Source: Danish Centre for Environment and Energy, University of Aarhus.

be used as a proxy for annual variations in population density (Whitlock, Aebischer, and Reynolds 2003). The number of animals killed, however, may depend on the effort expended by gamekeepers, and may reflect the hunting behaviour and legislation effective at a particular time (Baker, Harris, and White 2006; Kahlert et al. 2015). However, in this study fluctuations in the NGBR of red foxes were compared by age only within the period of the past 10 years. The open red fox hunting season lasts from the 1st of September to the 31st of January. Under certain conditions, culling is allowed throughout the year. Culled individuals are also included into the game bag records. Approximately 80% of the foxes recorded in the game bags are shot in October–January, and most of the remaining 20% are culled during the summer as cubs (Asferg, personal communication).

In Denmark, the outbreak of canine distemper in 2012 in the region of Jutland caused a severe decline (30%) in the National Game Bag Records for the 2013/2014 hunting season (Asferg 2014, 2016; Trebbien et al. 2014). As canine distemper occurred only in Jutland, the game bags of Jutland (GBRJ) were used as a relative measure for population density. From 2006 to 2012, GBRJ of the red fox ranged between 23,788 and 27,987 foxes per year; mean = 26,219 ± 565 SE (Figure 1). In the hunting season of 2013/2014, the GBRJ dropped by 38% (16,772 foxes) compared to the mean hunting bags of the previous five years (mean = 26,837 ± 507 SE). The record of the game bag of the 2013/2014 hunting season was the lowest in 67 years. In the hunting seasons of 2014/2015 and 2015/2016, GBRJ increased but were still 25% below the average (Figure 1). It is therefore expected that the fox population was below the carrying capacity from at least the spring of 2014 to 2016 (Figure 1).

The mean NGBR during the 1965–1977 period was higher than it is at present (mean = 53,931 ± 1130 SE foxes per year), but fox demography has been varying during this period. At that time juvenile foxes made up 67% of the foxes shot, while in the periods of 1997–2000 and 2012–2014, juveniles accounted for 54 and 56% of the foxes shot respectively, indicating a higher hunting pressure during the years 1965–1977 (Pagh et al. 2016).

Statistical analysis

The software PAST was used for all statistical analyses (Hammer, Haper, and Ryan 2001). One-way ANOVA and Kruskal-Wallis tests were used to assess differences in the mean and median, respectively, of weight and RFT of foxes between the periods and regions, and the weights of foxes in different age groups. The *t*-test and Mann-Whitney *U*-test were used to compare the mean and median, respectively, of weights of males and females, adults and subadults between periods, and the difference in the length of foxes between periods B and C.

Since skewed distributions may occur due to small sample sizes without being rejected by normality tests, both parametric tests, i.e. ANOVA and *t*-test, were used together with non-parametric tests (Kruskal-Wallis test and Mann-Whitney *U*-test). Sexual dimorphism was calculated as the percentage difference in either the mean length or the mean weight of males and females. The cube root of the mean body mass was used for the calculation of mass dimorphism.

Results

The mean weight of foxes was not found to be determined by the regions from which they had been sampled (Northern, Mid and Southern Jutland), therefore the data from different regions were pooled (Appendix 1).

Difference between time periods

Adult males from collections A and C were significantly heavier (mean weight \pm SE: 7.7 ± 0.3 kg and 7.5 ± 0.1 kg, respectively) compared to adult males from collection B (mean weight: 6.8 ± 0.2 kg, $F = 6.3$, $p < 0.01$, $H_c = 10.9$, $p < 0.01$). Results of the Mann-Whitney *U*-test (pairwise comparisons) were: $A > B$ $p < 0.002$ and $C > B$ $p < 0.01$ (Tables 1A and 1B). In collections A and C, adult males were significantly heavier than subadults (6.7 ± 0.1 kg

and 6.8 ± 0.2 kg, $t = 3.6$, $p < 0.001$, $z = 3.1$, $p < 0.01$ and $t = 3.9$, $p < 0.001$, $z = 3.8$, $p < 0.001$, respectively), while no significant difference was found between the body mass of adult and subadult males from collection B (6.6 ± 0.1 kg). The weight of adult females ($A = 6.0 \pm 0.1$ kg, $B = 6.1 \pm 0.2$ kg and $C = 6.2 \pm 0.1$ kg) did not differ significantly from that of subadult females ($A = 5.4 \pm 0.1$ kg, $B = 5.6 \pm 0.2$ kg and $C = 5.8 \pm 0.1$ kg) in any of the periods (Tables 1A and 1B).

Adult (114.4 ± 0.7 cm) and subadult male (113.0 ± 0.7 cm) foxes from collection C were significantly longer than adult (109.5 ± 1.0 cm) and subadult male foxes (109.1 ± 0.9 cm) from collection B ($t = 4.1$ $p < 0.001$, $z = 4.1$, $p < 0.001$ and $t = 3.6$, $p < 0.001$, $z = 3.6$, $p < 0.001$, respectively). No significant difference was found between the length of adult ($B = 105.3 \pm 0.8$ cm $C = 106.6 \pm 1.1$ cm) and subadult ($B = 103.7 \pm 0.8$ cm $C = 105.7 \pm 1.1$ cm) females in collections B and C (Tables 1A and 1B).

Sexual dimorphism

Significant sexual dimorphism was determined in all the three periods both in adults and subadults (Table 1A). Sexual dimorphism in body weight was relatively large both in adults and subadults in collections A (7.6% in adults) and (7.4% in subadults) and C (6.1% in adults) and

Table 1A. The mean weight and length \pm SE (standard error) of adult and subadult foxes in the three periods (1965–1977, 2012–2014 and the winter of 2015/2016) and significance level in sexual dimorphism for both adult and subadult foxes in the three periods (1965–1977, 2012–2014 and the winter of 2015/2016).

| Time period | Body mass (kg) | | Dimorphism (<i>t</i> -test/Mann-Whitney <i>U</i> -test between sex) | Length (cm) | | Dimorphism (<i>t</i> -test/Mann-Whitney <i>U</i> -test between sex) |
|---------------------------------|----------------------------|----------------------------|---|------------------------------|------------------------------|---|
| | <i>M</i> | <i>F</i> | | <i>M</i> | <i>F</i> | |
| A: 1965–1977 adult | 7.7 ± 0.3 ($n = 15$) | 6.0 ± 0.1 ($n = 16$) | $t = 7.6$ $t = 4.9$ $p < 0.0001$ $z = 3.6$ $p < 0.0003$ | 108.5 ± 1.1 ($n = 18$) | 102.9 ± 1.1 ($n = 17$) | $t = 5.2$ $t = 3.6$ $p < 0.001$ $z = -3.1$ $p = 0.002$ |
| A: 1965–1977 subadult | 6.7 ± 0.1 ($n = 46$) | 5.4 ± 0.1 ($n = 31$) | $t = 7.4$ $t = 5.8$ $p < 0.001$ $z = 5.0$ $p < 0.001$ | 109.3 ± 0.6 ($n = 49$) | 102.9 ± 0.5 ($n = 36$) | $t = 5.9$ $t = 7.4$ $p < 0.001$ $z = -6.0$ $p < 0.0001$ |
| B: 2012–2014 adult | 6.8 ± 0.2 ($n = 34$) | 6.1 ± 0.2 ($n = 46$) | $t = 3.6$ $t = 2.6$ $p = 0.02$ $z = 2.3$ $p = 0.02$ | 109.5 ± 1.0 ($n = 34$) | 105.3 ± 0.8 ($n = 40$) | $t = 3.8$ $t = 3.3$ $p = 0.002$ $z = 0.31$ $p = 0.002$ |
| B: 2012–2014 subadult | 6.6 ± 0.1 ($n = 49$) | 5.6 ± 0.2 ($n = 32$) | $t = 5.3$ $t = 4.4$ $p < 0.001$ $z = 3.7$ $p < 0.0002$ | 109.1 ± 0.9 ($n = 44$) | 103.7 ± 0.8 ($n = 33$) | $t = 4.9$ $t = 4.5$ $p < 0.0001$ $z = 4.5$ $p < 0.0001$ |
| C: Winter 2015/2016 adult | 7.5 ± 0.1 ($n = 42$) | 6.2 ± 0.1 ($n = 42$) | $t = 6.1$ $t = 7.3$ $p < 0.0001$ $z = 5.7$ $p < 0.0001$ | 114.4 ± 0.7 ($n = 41$) | 106.6 ± 1.1 ($n = 42$) | $t = 6.8$ $t = 7.5$ $p < 0.0001$ $z = 5.8$ $p < 0.0001$ |
| C: Winter 2015/2016 subadult | 6.8 ± 0.2 ($n = 60$) | 5.8 ± 0.1 ($n = 42$) | $t = 5.1$ $t = 5.3$ $p < 0.0001$ $z = 4.8$ $p < 0.0001$ | 113.0 ± 0.7 ($n = 59$) | 105.7 ± 1.1 ($n = 41$) | $t = 6.5$ $t = -6.0$ $p < 0.0001$ $z = 5.7$ $p < 0.0001$ |

Table 1B. Significance level between the mean weight and length of the two sexes of both adult and subadult foxes within and between three periods (1965–1977, 2012–2014 and the winter of 2015/2016).

| Time period | Body mass (kg) | | Length (cm) (only collection B and C) | |
|--|--|--|--|---|
| | M | F | M | F |
| A: 1965–1977 <i>t</i> -test/Mann-Whitney <i>U</i> -test between adults and subadults | <i>t</i> = 3.6 <i>p</i> < 0.001 <i>z</i> = 3.1 <i>p</i> < 0.01 | <i>t</i> = 1.8 <i>p</i> = 0.08 <i>z</i> = 1.9 <i>p</i> = 0.06 | <i>t</i> = 0.7 <i>p</i> = 0.50 <i>z</i> = 0.3 <i>p</i> = 0.71 | <i>t</i> = 0.0 <i>p</i> = 0.99 <i>z</i> = 0.17 <i>p</i> = 0.86 |
| B: 2012–2014 <i>t</i> -test/Mann-Whitney <i>U</i> -test between adults and subadults 2012–2014 | <i>t</i> = 1.1 <i>p</i> = 0.28 <i>z</i> = 0.8 <i>p</i> = 0.37 | <i>t</i> = 2.2 <i>p</i> = 0.03 <i>z</i> = 2.0 <i>p</i> = 0.05 | <i>t</i> = 0.3 <i>p</i> = 0.80 <i>z</i> = 0.1 <i>p</i> = 0.90 | <i>t</i> = 1.4 <i>p</i> = 0.18 <i>z</i> = 1.2 <i>p</i> = 0.24 |
| C: Winter 2015/2016 <i>t</i> -test/Mann-Whitney <i>U</i> -test between adults and subadults Winter 2015/2016 | <i>t</i> = 3.9 <i>p</i> < 0.001 <i>z</i> = 3.8 <i>p</i> < 0.001 | <i>t</i> = 2.2 <i>p</i> = 0.05 <i>z</i> = 1.8 <i>p</i> = 0.08 | <i>t</i> = 1.4 <i>p</i> = 0.17 <i>z</i> = 0.9 <i>p</i> = 0.36 | <i>t</i> = 0.7 <i>p</i> = 0.51 <i>z</i> = 0.12 <i>p</i> = 0.90 |
| Between periods | <i>F</i> = 6.3 | <i>F</i> = 0.3 | <i>t</i> = 4.1 | <i>t</i> = 1.2 |
| Adult | <i>p</i> < 0.01 | <i>p</i> = 0.77 | <i>p</i> < 0.0001 | <i>p</i> = 0.23 |
| One-way ANOVA and Kruskal Wallis | Hc = 10.9 | Hc = 0.58 | <i>z</i> = 4.1 | <i>z</i> = 1.1 |
| Between periods | <i>p</i> < 0.01 | <i>p</i> = 0.75 | <i>p</i> < 0.0001 | <i>p</i> = 0.27 |
| Subadult | <i>F</i> = 0.4 | <i>F</i> = 2.2 | <i>t</i> = 3.6 | <i>t</i> = 1.4 |
| One-way ANOVA/Kruskal Wallis | <i>p</i> = 0.68 | <i>p</i> = 0.12 | <i>p</i> < 0.001 | <i>p</i> = 0.15 |
| | Hc = 0.79 | Hc = 4.4 | <i>z</i> = 3.6 | <i>z</i> = 2.2 |
| | <i>p</i> = 0.67 | <i>p</i> = 0.11 | <i>p</i> < 0.001 | <i>p</i> < 0.03 |

(5.1% in subadults) compared to dimorphism in collection B, where dimorphism in subadults (5.3%) was larger than dimorphism in adults (3.6%). The same pattern of dimorphism was found in relation to fox length (Tables 1A and 1B).

Rump fat thickness

RFT was available only from collections B and C. In winters of 2012–2014, no significant difference was found in RFT across sexes and age classes (*F* = 1.9 *p* = 0.14, Hc = 7.0, *p* = 0.07), but adult females were found to be significantly fatter than adult males (Mann-Whitney’s pairwise comparison *p* < 0.01) (Table 2). In contrast, in the winter of 2015/2016, significant differences were found in RFT (*F* = 6.5 *p* < 0.001, Hc = 17.9 *p* < 0.001) (Table 2), which was larger in adult females than in adult males (*p* < 0.0001) and subadult females (*p* < 0.01), and RFT was larger in subadult females than in subadult males (*p* < 0.02) (Table 2). Adult females had significantly more

RFT in the winter of 2015/2016 than in winters of 2012–2014 (*t* = 2.1; *p* < 0.05, *z* = 3.8 *p* < 0.05).

Difference in weight between age groups

This study has revealed an overall tendency for older foxes to be heavier than foxes in younger age groups (Figure 2). However, in collection C, the oldest male foxes (M3+) were not larger than male foxes aged 1 or 2 years, and in collection B, subadult males were relatively large (Figure 1). Significant differences in weight between age groups were determined for males in all periods: 1965–77; *F* = 7.8 *p* < 0.001, *z* = 14.5 *p* < 0.01, 2012–14; *F* = 3.3 *p* < 0.05, *z* = 6.3 *p* = 0.10 and 2015/2016; *F* = 5.2 *p* < 0.01, *z* = 16.6 *p* < 0.001. In addition, the weight of females in different age groups differed significantly: 1965–1977 (*F* = 3.7; *p* < 0.02, *z* = Hc = 7.4; *p* < 0.06, 2012–2014 (*F* = 3.4 *p* < 0.05; *z* = 8.4; *p* < 0.05) and 2015/2016 (*F* = 5.6; *p* < 0.01, *z* = 10.8; *p* < 0.02).

Table 2. Mean rump fat thickness (RFT) ± SE (standard error) in male and female, adult and subadult foxes.

| Period | RFT (cm) adult | | RFT (cm) subadult | | Test (one-way ANOVA/ Kruskal Wallis) | Mann-Whitney <i>U</i> -test |
|--|--|--|--|--|---|--|
| | M | F | M | F | | |
| Winters 2012–2014 | 0.47 ± 0.06 (<i>n</i> = 29) | 0.64 ± 0.04 (<i>n</i> = 50) | 0.59 ± 0.05 (<i>n</i> = 50) | 0.56 ± 0.05 (<i>n</i> = 40) | <i>F</i> = 1.9 <i>p</i> = 0.14 Hc = 7.0 <i>p</i> = 0.07 | AdF > AdM <i>p</i> < 0.01 |
| Winter 2015/2016 | 0.58 ± 0.05 (<i>n</i> = 37) | 0.77 ± 0.05 (<i>n</i> = 36) | 0.51 ± 0.04 (<i>n</i> = 52) | 0.67 ± 0.05 (<i>n</i> = 31) | <i>F</i> = 6.5 <i>p</i> < 0.001 Hc = 17.9 <i>p</i> = 0.001 | AdF > AdM, <i>p</i> < 0.0001 AdF SubM, <i>p</i> < 0.01 SubF > SubM, <i>p</i> < 0.02 |
| <i>t</i> -test/Mann-Whitney <i>U</i> -test | <i>t</i> = 1.4 <i>p</i> = 0.16 <i>z</i> = 1.6 <i>p</i> = 0.12 | <i>t</i> = 2.1 <i>p</i> < 0.04 <i>z</i> = 3.8 <i>p</i> < 0.05 | <i>t</i> = 1.4 <i>p</i> = 0.17 <i>z</i> = 1.3 <i>p</i> = 0.19 | <i>t</i> = 0.92 <i>p</i> = 0.36 <i>z</i> = 0.89 <i>p</i> = 0.37 | – | – |

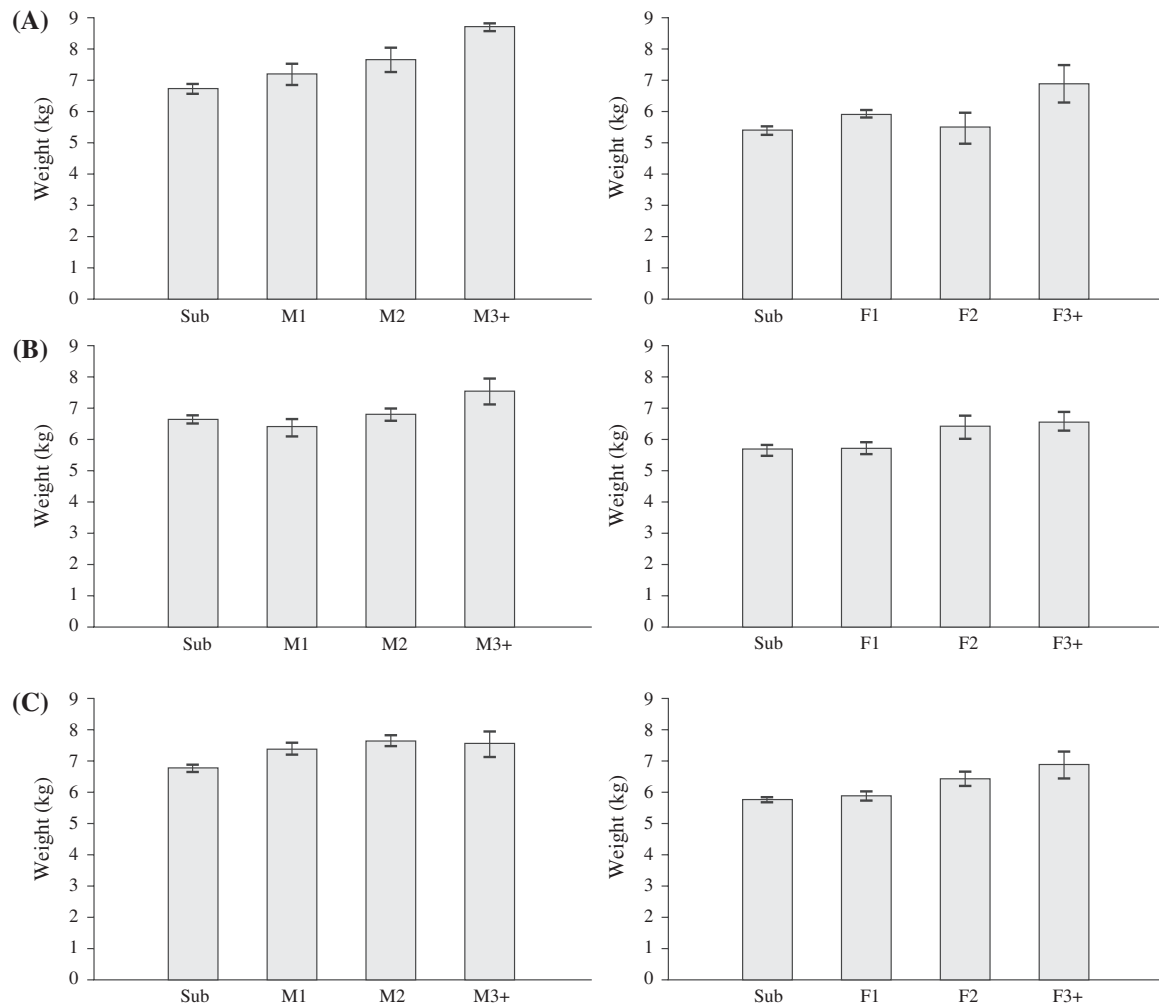


Figure 2. Bar charts with Standard Error whiskers showing mean weights of male and female foxes in different age groups in the three periods: (A) (1965–1977), (B) (2012–2014) and (C) (2015/2016). The categories are: subadult males (M sub); 1-year-old males (M1); 2-year-old males (M2); males at and over the age of 3 (M3+); subadult females (F sub); 1-year-old females (F1); 2-year-old females (F2); females at and over the age of 3 (F3+).

Discussion

Body size in relation to population density

The mean weight of male foxes within the same geographical area was found to fluctuate over time. Adult males were significantly heavier during the periods of low population density due to hunting or canine distemper, i.e. in the 1965–1977 period and in the winter of 2015/2016 (mean weight \pm SE: 7.7 and 7.5 kg, respectively), than in the period 2012–2014 (mean weight 6.8 kg) (Table 1A). No significant differences in weight were found in females; hence sexual dimorphism varied over time. Similarly, significant regional differences in the body mass of male foxes, but not in that of females, were recorded among fox populations in Italy (Cavallini 1995). Males were both longer and heavier in the northern regions of Italy than in southern parts, whereas females were slightly longer, but not heavier in the north than in the south, hence variation in size depended on population density rather than on climate or the availability of food (Cavallini 1995). This is in agreement with

the present study, wherein climate and geographical position are fixed parameters, although minor climate changes in temperature and precipitation have occurred over the past 50 years. Adult males were apparently able to respond to the advantage of density reduction and the expected lower competition for food among the surviving foxes. The body mass of British male foxes has been reported to exhibit a stronger relationship with July rainfall ('worm nights') than the female body mass (Soulsbury et al. 2008). The fact that the female body mass does not increase as much as the male body mass during years of ample food indicates that the two sexes are subject to different selection forces as suggested by Soulsbury et al. (2008). This was supported by a study on foxes in Bristol (UK), where heavier males were found to hold larger territories, exert a greater boundary pressure on smaller neighbours, and to invest more effort when searching for extra mates by traversing a wider area (Iossa et al. 2008). In contrast, the body mass of females was not related to the territory size, probability of breeding, litter size, or cub mass (Iossa et al. 2008).

Older foxes are heavier

Older male foxes were found to be heavier than those in younger age groups (Figure 2). This may reflect some selection for large males, which may have an advantage in agonistic fights for both food and mates (Iossa et al. 2008). Although it cannot be excluded that older foxes may be larger than young foxes as a result of their extra experience as hunters, particularly in periods of high population density and/or low availability of food.

As an exception, male foxes from the age group M3+ collected during the winter of 2015/2016 were not larger than individuals belonging to younger age groups (Figure 2(C)). This may be because the foxes that were over 2 years of age and were collected this winter matured during high-density years when food availability was more restricted. In contrast, the relatively heavy subadults collected in 2012–2014 (Figure 2(B)) may have taken advantage of low population density resulting from the distemper outbreak in the early summer of 2012.

RFT and population density

In the winter of 2015/2016, when fox population density was low, adult females had particularly large RFT deposits (mean = 0.77 cm \pm 0.05) compared to those of adult males (mean = 0.58 cm \pm 0.05) and subadult males (0.51 \pm 0.04) (Table 2). This was in contrast to winters of 2012–2014, when no significant differences were found in RFT between males and females as well as between adult and subadult individuals (Table 2). Adult females had significantly more RFT in the winter of 2015/2016 than in winters of 2012–2014 (mean = 0.64 \pm 0.04) when population density was high. Hence, it is likely that in low-density populations, females encounter less competition for food from males which are generally larger as has been suggested by Cavallini (1998).

Reasons for sexual dimorphism in foxes

Significant sexual dimorphism was found in male and female foxes in all the three periods both in adults and subadults (Table 1A).

Sexual dimorphism is known to be particularly pronounced in small species of the family Mustelidae. Two explanations for the large sexual dimorphism in mustelids have been proposed: (1) Intersexual competition for food is reduced by dimorphism, as each sex can exploit different prey and diet (Moors 1980). (2) In polygynous breeding, where females raise their litter alone, small females are favoured because they need less energy for daily maintenance. In contrast, larger males are favoured due to their ability to exploit a wider range of prey. The optimum size of each sex is therefore a result of different selective pressures (Moors 1980), and larger males may be favoured when competing for a mate (Abramov and

Puzachenko 2005). The degree of sexual dimorphism can be viewed as an indication of the intensity of competition for females within a species (Korablev, Korablev, and Korablev 2013).

Although adult males and juvenile foxes were found to have a larger food-niche breadth than adult females, their diets have a considerable overlap (Kidawa and Kowalczyk 2011), and it is unlikely that hypothesis 1) can explain sexual dimorphism in foxes.

The social organisation of the red fox varies from monogamous pairs to small or medium-sized groups, and mating systems range from monogamy to polygynous or polygynandrous groups, as well as groups with unrelated animals (Baker 2004; Macdonald 1983; Zabel 1986). In most groups, only one female will breed, but social groups with a higher number of breeding females have been observed (Storm and Ables 1966; Zabel and Taggart 1989). Sexual dimorphism in foxes may allow male foxes to benefit from polygynous mating, potentially explaining some of the variation found in mating systems (Iossa et al. 2008), at least partly supporting hypothesis 2). In support of this, sexual dimorphism is either small or absent in monogamous species such as racoon dogs *Nyctereutes procyonoides* and crab-eating foxes *Cerdocyon thous* (Kauhala 1998; Macdonald and Courtenay 1996).

Dimorphism and population density

In the present study, sexual dimorphism was found to be larger during periods of high population density. Sexual dimorphism in body weight was relatively large in 1965–1977 both in adults (7.6%) and subadults (7.4%) and in 2015/2016 in adults (6.1%) and in subadults (5.1%) compared to the 2012–2014 period, when the population density was low and dimorphism in adults reached 3.6% and in subadults 5.3% (Table 1A).

If large dimorphism relates to the polygamous mating system, the question is if foxes tend to be more polygynous at a low population density. However, in dense populations, e.g. urban populations, and also in periods of ample food (Baker et al. 2000; Lindström 1983; Macdonald 1983), foxes seem to shift from monogamy to polygynous groups. The basic social group of red foxes may therefore be polygynous and may not exclusively be explained by population density and resource availability.

Conclusion

The change in body size of Danish male foxes, but not in that of female foxes, was found to relate to population density. Males were found to be relatively larger in years of low population density and *vice versa*. Further studies into the inter-annual fluctuations in body size of male foxes are needed in order to fully understand the

underlying mechanisms and the subsequent effects of fluctuating sexual dimorphism.

Competing interests

The authors declare that they have no competing interests.

Ethics approval and consent to participate

All applicable international, national, and institutional guidelines for the care and use of animals were followed. No ethical approval was required from an institutional or national ethics review board. The study complies with current Danish laws. No animals were sacrificed for the purposes of this study. The research was carried out as part of the regular surveillance and monitoring of wildlife diseases by the National Veterinary Institute Danish Technical University, Section for Diagnostics and Scientific Advice, Copenhagen.

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Appendix 1. Mean weight \pm SE (standard error) of foxes in three different regions (Northern, Mid and Southern Jutland).

| Regions | BM (kg) adult | | BM (kg) subadult | |
|---------------------|---------------|---------------|------------------|---------------|
| | M | F | M | F |
| 2012–2014 | 7.0 \pm 0.2 | 6.0 \pm 0.2 | 6.7 \pm 0.1 | 5.5 \pm 0.2 |
| Mid Jutland | (n = 28) | (n = 40) | (n = 42) | (n = 29) |
| 2012–2014 | 5.8 \pm 0.3 | 7.0 \pm 0.3 | 5.9 \pm 0.3 | 6.5 \pm 1.1 |
| Southern Jutland | (n = 6) | (n = 6) | (n = 7) | (n = 3) |
| t-test/ | t = 2.9 | t = 2.4 | t = 2.3 | t = 1.6 |
| Mann-Whitney U-test | p = 0.01 | p < 0.05 | p < 0.05 | p = 0.45 |
| | z = 2.9 | z = 2.4 | z = 2.4 | z = 1.0 |
| | p < 0.01 | p < 0.05 | p < 0.02 | p = 0.30 |
| Winter 2015/16 | 7.4 \pm 0.4 | 5.8 \pm 0.2 | 6.4 \pm 0.3 | 5.6 \pm 0.3 |
| Northern Jutland | (n = 6) | (n = 8) | (n = 9) | (n = 7) |
| Winter 2015/16 | 7.4 \pm 0.2 | 6.5 \pm 0.2 | 6.7 \pm 0.2 | 5.8 \pm 0.1 |
| Mid Jutland | (n = 24) | (n = 19) | (n = 25) | (n = 16) |
| Winter 2015/16 | 7.5 \pm 0.2 | 5.9 \pm 0.2 | 7.1 \pm 0.2 | 6.2 \pm 0.3 |
| Southern Jutland | (n = 7) | (n = 9) | (n = 21) | (n = 9) |
| One way ANOVA/ | F = 0.009 | F = 3.3 | F = 1.7 | F = 1.4 |
| Kruskal-Wallis test | p = 0.99 | p = 0.05 | p < 0.19 | p = 0.25 |
| | Hc = 1.7 | Hc = 6.44 | Hc = 3.9 | Hc = 2.54 |
| | p < 0.41 | p < 0.05 | p = 0.14 | p = 0.28 |