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*Published in:*
Genetics and Biodiversity Journal

*Publication date:*
2018

*Document Version*
Publisher's PDF, also known as Version of record

*Citation for published version (APA):*
Pagh, S., Chriél, M., Jensen, B., Pertoldi, C., & Hansen, M. S. (2018). Development of body mass and sexual size dimorphism in Danish red foxes (Vulpes vulpes). *Genetics and Biodiversity Journal*, *2*(1), 36-47. http://ojs.univ-tlemcen.dz/index.php/GABJ/article/view/291

Genetics and Biodiversity Journal

Journal homepage:http://ojs.univ-tlemcen.dz/index.php/GABJ

Original Research Paper

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# DEVELOPMENT OF BODY MASS AND SEXUAL SIZE DIMORPHISM IN DANISH RED FOXES (*VULPES VULPES*)

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**Article history:** Received: 05 December 2017, Revised: 25 December 2017, Accepted: 25 January 2018

## Abstract

In this study, we examine the development of body mass and sexual size dimorphism (SSD) in 178 juvenile wild Danish red foxes from 99 litters using piecewise analyses of regression lines for age *versus* weight. When fox cubs are younger than 100 days, only slight (SSD=1.7%) and no significant difference (t-test: t=1.2, p=0.24) was found in the mean weight of males (2.03± kg) and females (1.93± kg), and no significant difference was found in the slope of regression lines for males and females (F=0.97E-5, p = 0.99). In the growth period between 100 days of age and mating around 275 days of age, the regression line in males steepens more than that of females (difference in slopes, F=5.9, p<0.02) and the difference in mean weight of the sexes become highly significant (SSD=7.4%, difference in mean t=4.6, p=2.2E-5). After mating the growth curve levels off i.e. the slope of the regression lines for age *versus* weight is not significantly different from zero. Yearly variation was revealed in the growth rate of juvenile foxes (difference in slope for males; F=3.9, p<0.01 and females; F=8.6, p<0.001).
Conclusion: SSD in red foxes mainly develop as a result of a faster grow rate in males between indepency and maturity. Ontogony of red foxes may genetically be disposed to prevent males outcompeting females in the early stages of life (<100 days), when cubs are still fed by adults and the increase in SSD before mating, may be an adaption to selective forces benefitting larger males. The growth rate of juvenile foxes of both sexes is influenced by environmental variation in different years.
**Key words**: body size, weight, cubs, ontogeny, sexual size dimorphism.

## Introduction

The ontogeny of mammals depend not only on nutrition, but also on genetically predispositions linked to life strategies of the species. Within mammals, males are usually larger than females of the same species (Swanson et al., 2013). Sexual size dimorphism (SSD) is known to be particularly male biased (males being larger than females) in the orders of Pinnipeds (seals, sea lions and walruses), in northern elephant seals (*Mirounga angustirostris*) and the small species of the family Mustelidae e.g. weasel (*Mustela nivalis*), stoat (*M. ermine*) and American mink (*M. vison*) (Moors, 1980; Thom et al., 2004; Cassini, 2017). But, also within mammals, exceptions exist, e.g. SSD is either small or absent in the monogamous species, racoon dogs (*Nyctereutes procyonoides*) and crab-eating foxes (*Cerdocyon thous*) (Macdonald & Courteney, 1996 ;Kauhala, 1998) and female biased in the promiscuous mating cliff chipmunks (*Tamias dorsalis*) and the polygynous spotted hyena (*Crocuta crocuta*) (Frank, 1986; Swanson et al., 2013; Kilanowski et al., 2016).

### *Selection of SSD in mammals*

Male biased SSD may occur if fecundity selection in females involves a cost that increases as body size increases, then selection will go towards smaller females, and the larger body size of males may simply be an effect of females getting smaller (Cassini, 2017). Especially in larger mammals, female life-history parameters related to fecundity are slower or energetically more costly; hence, natural selection in general favors small body size in mammal females (Cassini, 2017). Small females may be favoured because they need less energy for the daily maintenance. By reducing their own energy requirements females can channel more into reproduction (Moors 1980; Thom et al. 2004). However, selection for larger males may also occur if males benefit from a larger body in agonistic fights over territory or mates (Iossa et al., 2008; Cassini, 2017).

In most other species than mammals, the size of females has been hypothesized to be positively correlated to fecundity, referred to as the “fecundity hypothesis” (Fairbairn, 1997; Fairbairn, 2005).. However, for mammals, female biased SSD in mammals may rather be related to competition for males or for resources such as territory or food rather than fecundity (Kilanowski, et al., 2016).

According to Thom et al., (2004), there are mainly three explanations for SSD: 1) Sexual selection, expressed either as competition for mates or as mate choice. A larger body size in males may be selected for due to dominance benefits, and hence increased mating opportunities. According to Korablev et al. (2013), the degree of male biased SSD can be viewed as an indication of the degree of competition for females within a species. 2) Intrinsic differences in the reproductive roles of males and females could result in SSD, e.g. female mustelids may be small partly because it is more energetically efficient for reproduction (see also Moors, 1980). 3) SSD could arise through niche separation among the sexes of significantly different size, i.e. reducing competition for food between males and females. The optimum size of each sex is therefore a result of different selective pressures (see also McDonald, 2002).

### *Ontogeny of SSD in mammals*

In some species, sexual dimorphism in body mass occurs before or soon after birth, e.g. in earless-and true seals (Kovacs et al., 1986), whereas other species develop SSD when they approach sexual maturity, e.g. in bighorn sheep (*Ovis Canadensis*) and cliff chipmunk (*Tamias dorsalis*) (Festa-Bianchet et al., 2000; Kilanowski et al., 2016). In cliff chipmunks, SSD is female biased. In this species, females and males are the same size at birth, but within two months, a clear difference is evident between the sexes (Kilanowski et al., 2016). Similar ontogeny of SSD was found in bighorn sheep (*Ovis Canadensis*), where juveniles are identical in size at birth, but within three months, males become heavier than females (Festa-Bianchet et al., 1996). Some species do not develop SSD until after the first reproductive event, e.g. female southern flying squirrels (*Glaucomys volans*) are larger than males, nevertheless females were not significantly larger or heavier than males at first reproduction, but were about 7% heavier and 22% larger than males at the second breeding (Fokidis et al., 2007).

In mammals, SSD typically appears after gonadal differentiation in connection with the production of sex-related hormones, such as estradiol and testosterone. These hormones influence both the expression of sex-specific phenotypes as well as sex-specific behaviours by changing brain functions (Kimura & Matsuyama, 2012).

O'Mara (2012) defines three different pathways for the ontogeny of SSD: 1) The most common and simplest way to SSD is “bimaturism” where one sex grow for a longer period of time than the other, but at the same rate, e.g. in haplorrhine monkeys males grow for 10% longer time than females. Bimaturism may be a response to strong intrasexual (male) competition where access to mates is related to body size. 2) Males and females grow at different rates for the same duration, e.g. if males grow at a faster rate, SSD will be male biased. Rate differences occur at the end of the growth period near the onset of sexual maturity that greatly accelerates body mass growth. 3) A combination of rate and duration differences may produce SSD in adults. Rate and duration of growth may respond to selection independently of each other, and the combination of rate and timing differences of males and females may reflect complex interactions of both intrasexual and intersexual competition.

Studies of the size of adult red foxes (*Vulpes vulpes*) show that SSD is male biased and that average SSD ranges between 4.4% and 7.7% in Europe and North America and that SSD may not only vary geographically, but also locally during different time periods (Cavallini, 1995; Pagh et al., 2017).

The weight of fox cubs in the wild are difficult to obtain, and to our knowledge, there has not been any evaluation of the ontogeny of body mass and SSD in wild foxes. Most previous studies of cub weights are from foxes held under semi natural conditions (Storm et al., 1966; Storm, 1976; Sargeant 1978). Others present data on the weight of juvenile red foxes, but they do not separate males from females, hence SSD cannot be interpreted (Vogtsberger et al., 1973; Kolb & Hewson, 1980a).

### *Aims of the investigation*

The aims of this study is: 1) To present rare data on the ontogeny of Danish red fox cubs and 2) to examine if development of SSD in red foxes is a result of different growth rates of the sexes or due to bimaturism, 3) to test if the development of body mass of juvenile foxes is influenced by yearly environmental conditions and 4) to discuss possible life history strategies behind the ontogeny of red foxes.

## Materials and methods

Data on the weight of foxes from the period 1965-1977 were found alongside their associated 202 skeletons (no. 13000 to 13202) at the Natural History Museum, Aarhus. Of these, 178 individuals from 99 litters had been ear tagged as cubs or juveniles (less than one year) in a mark-recapture study by (Jensen, 1973). The foxes were mainly from the Danish peninsula of Jutland: 128 from Mid Jutland; 19 from Northern Jutland; 10 from Southern Jutland. In addition, 19 were from the island of Zealand and two were from the island of Bornholm. The majority of the recaptured foxes (152) were shot during hunting, 12 were found newly dead or put down, eight were killed by cars or harvesters, three were killed by dogs and three died of other causes. Ten of the recovered foxes, which were found dead were removed from the data set, to prevent bias in mean weights due to illness or decomposing. Individuals were weighed when ear tagged (170 cubs) and later when they were recovered dead.

The birth date of red foxes in Denmark has not been studied, yet based on Lloyd & Englund, 1973(1973) and the latitude of Denmark, we can assume that most cubs are born between mid-March and the first week of April. The age of each fox was estimated as the number of days between 1st April in the year that the cub was ear tagged and the time of death. Foxes less than six months old were classified as cubs (Harris & Trewhella, 1988), and foxes less than one year as juveniles.

The software PAST was used for statistical analyses (Hammer et al. 2001). The main data set was not normally distributed due to the sampling method; Data were collected in two main periods 1) cubs (caught for earmarking) mainly within their first eight weeks of life or adults (recovered) mainly more than six month of age. The red fox in Denmark is protected by law during the breeding season from February to September. Therefore, few foxes were recovered during their first six months of life.

To understand how growth rate affects the development of body mass and SSD, a piecewise regression model was fitted to the data following O'Mara, (2012). To describe the ontogeny of red foxes three growth periods were chosen:

1. Between birth and 100 days of age, the duration of this period was based on the development of the regression lines of males and females with 95% confidence interval.

2. From 100 days of age to the first mating (i.e. sexual maturity). Oestrus starts in Danish foxes in December, hence around 275 days of age (Lloyd, 1980).

3. From sexual maturity (275 days) to one year of age.

Data within the three growth periods were normally distributed (tested by Shapiro-Wilk's test; p(normal)<0.15, between 100 and 275 days; p(normal)<0.11 and between 275 and one year; p(normal)<0.93. *t*-test was used to compare the mean weights of males and females.

Least square and Generalized Linear Model (GLM) was used to examine the age *versus* weight of the three periods and association between male and female age *versus* weight (SSD). The slopes of the regression lines were compared by Pearsons- product-moment correlation test and ANCOVA. Also, possible yearly variations in growth development of juveniles (within their first year) between the years 1966-1969 (only years with data from minimum ten litters in one year) were examined using Least square regression and GLM. Regression lines were tested for differences in slope and intercept. SSD was calculated as the percent difference between the cube root of the mean weight of males and females following Cavallini, (1995).

## Results

*Growth period 1. Cubs younger than 100 days of age*

**Table 1.** Ontogeny of body mass of male (M) and female (F) Danish red foxes and SSD in three different growth periods; 1) 1st April to mid-June, cubs feed by adults at the den. 2) Mid-June to December. From independency of cubs to mating season. 3) December to 1st April. Mating and breeding season. N = number of weight data, A denotes ANCOVA and GLM Generalized linear model. S.E. =standard error mean. SSD = % of difference between the square root in body mass of males and females.

| | **Growth period 1 (<100 days of age)** | | **Growth period 2 (100> <275 days)** | | **Growth period 3 (275> <365 days)** | |
|---|---|---|---|---|---|---|
| | **M** | **F** | **M** | **F** | **M** | **F** |
| N | 97 | 69 | 37 | 28 | 15 | 13 |
| **Slope** | | | | | | |
| ***Least square*** | 0.0294 | 0.0293 | 0.0219 | 0.0132 | -0.0099 | -0.0201 |
| ***GLM*** | 0.0294 | 0.0293 | 0.0219 | 0.0132 | -0.0099 | -0.0201 |
| **Intercept** | | | | | | |
| ***Least square*** | 0.5852 | 0.5255 | 1.8853 | 2.504 | 9.709 | 11.495 |
| ***GLM*** | 0.5852 | 0.5255 | 1.8853 | 2.504 | 9.709 | 11.495 |
| **$R^2$** | 0.34 | 0.35 | 0.63 | 0.54 | 0.05 | 0.21 |
| **Comparison between slopes** ***ANCOVA*** | F=1,97E-5<br>p=0.99 | | F=5.85<br>p<0.02 | | F=0.31<br>p<0.58 | |
| **GLM p(slope=0)** | 3.9E-12 | 2.8E-9 | 2.6E-15 | 3.2E-8 | 0.41 | 0.09 |
| **Mean weight (±S.E.) kg** | 2.03 (±0.07) | 1.93 (±0.07) | 6.3 (±0.20) | 5.0 (±0.19) | 6.7 (±0.23) | 5.4 (±0.19) |
| **T-test** | *t*=1.2, *p*=0.24 | | *t*=4.6, *p*<2.2E-5 | | *t*=5.3, *p*<2.9E-6 | |
| **SSD** | 1.7% | | 7.4% | | 6.9% | |

The average weight of cubs caught between 23 days and one month of age from 1st April was 1.3±0.1S.E. kg (range 0.8-1.7, n=13). The mean weight of foxes younger than around 100 days old was 2.03±0.1S.E. kg for males (n=96) and 1.93±0.1S.E. kg for females (n=71), hence SSD=1.7%. No significant difference in mean body weight between males and females was detected at this stage of life (t=1.2, p=0.24, t-test) (Table 1). Likewise, the slopes of the regression lines for male and female cubs younger than 100 days old did not differ significantly (*F*=1.97E-5, *p*=0.99) (Table 1). The slope and intercept found by least square regression lines and GLM was identical (Table 1).

*Growth period 2. Juveniles between 100 days of age and mating (275 days)*

The mean weight between 100 days of age and mating was 6.3±0.2S.E. kg for males (n=37) and 5.0±0.2S.E. kg for females (n=28) (SSD=7.4%). The difference in mean body weight between males and females was highly significant (t=4.6, p<2.2E-5, t-test) (Table 1). The slope of the regression lines for age versus weight for males and females in this growth period differed significantly (F=5.9 p <0.02) with a steeper slope for male foxes than for females (Table 1). The GLM regression lines were identical to least square regression lines (Table 1).

*Growth period 3. From mating to one year of age*

The mean weight of foxes between 275 days of age and one year was 6.7±0.2S.E. kg for males (n=15) and 5.4±0.2S.E. kg for females (n=13). The difference in mean body weight between males and females was significant (SSD =6.9%, $t$=5.3, $p$<2.9E-6, $t$-test) (Table 1). During this growth period, the slopes of the regression lines for both males (- 0.0099) and females (-0.0201) were marginally negative. For both sexes the slopes of the regression lines were not significantly different from zero; p (slope=0)<0.41, GLM and p (slope=0)<0.09, GLM, for males and females, respectively (Table 1). Although the growth curve levels off in this period, one-year-old foxes were found to be slightly heavier than juvenile foxes between 275 days and one year; mean weight of one-year-old males and females were 7.2 ±0.3S.E kg and 5.9 ±0.1S.E kg, respectively.

*Yearly variation in the body size of juvenile foxes*

**Table 2A**. The slope and intercept of regression lines for age *versus* weight for juvenile Danish red fox males during the years 1966 to 1969, using GLM Generalized linear model.

| **Year** | **No. of litters** | **Slope** | **Intercept** | **G** | **P(slope=1)** |
|---|---|---|---|---|---|
| 1966 | 13 | 0.024 | 0.57 | 220.98 | 5.5E-50 |
| 1967 | 10 | 0.020 | 1.27 | 32.10 | 1.5E-8 |
| 1968 | 27 | 0.018 | 1.73 | 154.09 | 2.2E-35 |
| 1969 | 38 | 0.023 | 0.94 | 623.00 | 1.6 E-137 |

**Table 2B.** Significance table for males. Comparisons of slopes and intercepts of regression lines for age *versus* weight of juvenile male red foxes in the years 1966 to 1969. The upper cells show the tests for differences in slope, and the lower cells show the tests for differences in intercept. L= number of litters, N=data points

| Year<br>Slope/<br>Intercept | 1966<br>L=13<br>N = 32 | 1967<br>L=10<br>N = 13 | 1968<br>L=27<br>N = 34 | 1969<br>L=38<br>N = 68 |
|---|---|---|---|---|
| 1966 | | $F = 1.9$<br>$p = 0.17$ | $F = 7.8$<br>$p < 0.01$ | $F = 0.40$<br>$p < 0.53$ |
| 1967 | $F = 3.7$, $p = 0.19$<br>$t = 2.0$, $p = 0.05$ | | $F = 0.17$<br>$p = 0.68$ | $F = 2.16$<br>$p = 0.15$ |
| 1968 | $F = 1.2$, $p = 0.54$<br>$t = 3.2$, $p < 0.003$ | $F = 2.8$, $p = 0.03$<br>$t = 0.7$, $p = 0.50$ | | $F = 9.7$<br>$p < 0.01$ |
| 1969 | $F = 2.0$, $p < 0.02$<br>$t = 1.4$, $p = 0.22$ | $F = 4.4$, $p = 0.0001$<br>$t = 0.8$, $p = 0.41$ | $F = 1.6$, $p = 0.11$<br>$t = 3.2$, $p < 0.002$ | |

Yearly variation in the slopes of the regression line for age *versus* weight was found for both sexes of juvenile foxes in the years from 1966 to 1969 (males; F=3.9, p<0.01, females; F=8.6, p<0.001), hence cubs grew faster in some years than others. Also, the intercepts differed significantly from year to year indicating a difference in the birth weight of cubs between the years.

For juvenile males, the slope of the regression line for age versus weight was steeper in 1966 than in 1968 (F= 7.8, p < 0.01), and the intercept for 1966 was lower than in 1967 (F = 3.7, p = 0.19, t = 2.0, p =0.05) and 1968 (F = 1.2, p = 0.54 t = 3.2, p < 0.003), although only marginally significantly different from 1967 (Figure 2A, Table 2A and 2B). Also, the slope and intercept of the regression lines for 1968 and 1969 differed significantly (F = 9.7 p < 0.01, F = 1.6, p = 0.11, t = 3.2, p < 0.002) (Figure 2A, Table 2A and 2B).

For juvenile females, the slope of the regression line for age *versus* weight was significantly steeper in 1966 than in all other years (1967; F=18.6, p<0.001, 1968; F=35.7, p<3.4E-7, 1969; F=8.7, p< 0.01), and the intercept of 1966 was lower than that of all other years (1967; *t*=18.6, p=0.05, 1968; *t*=5.1, p<7.0E-6, 1969; *t*=2.7, p< 0.01), however, the intercept of 1966 was only marginally significantly different from 1967 (Figure 2B, Table 3A and 3B). The intercept of 1967 was significantly lower than the intercept of 1968 (t=2.7, p<0.01) (Figure 2B, Table 3A and 3B).

**Table 3A**. The slope and intercept of regression lines for age *versus* weight for juvenile Danish red fox females during the years 1966 to 1969, using GLM Generalized linear model.

| **Year** | **No. of litters** | **Slope** | **Intercept** | **G** | **P(slope=1)** |
|---|---|---|---|---|---|
| 1966 | 13 | 0.025 | 0.29 | 168.66 | 1.5E-38 |
| 1967 | 10 | 0.016 | 1.03 | 147.36 | 6.5E-34 |
| 1968 | 27 | 0.013 | 1.72 | 202.77 | 5.2E-46 |
| 1969 | 38 | 0.017 | 1.31 | 111.18 | 5.4E-26 |

**Table 3B**. Significance table for females. Comparisons of slopes and intercepts of regression lines for age *versus* weight of juvenile female red foxes in the years 1966 to 1969. The upper cells show the tests for differences in slope, and the lower cells show the tests for differences in intercept.

| **Year Slope/ Intercept** | **1966 N = 15** | **1967 N = 16** | **1968 N = 34** | **1969 N = 34** |
|---|---|---|---|---|
| 1966 | | *F* = 18.6<br>*p* <0.001 | *F* = 35.7<br>*p*< 3.4E-7 | *F* = 8.7<br>*p* <0.01 |
| 1967 | *F* = 1.5, *p* < 0.47<br>*t* = 2.0, *p* = 0.05 | | *F* = 1.8<br>*p* = 0.18 | *F* = 0.2<br>*p* = 0.61 |
| 1968 | *F* = 1.9, *p* < 0.13<br>*t* = 5.1, *p*< 7,0E-6 | *F* = 1.1, *p* = 0.80<br>*t* = 2.7, *p* < 0.01 | | *F* = 3.1<br>*p* = 0.08 |
| 1969 | *F* = 1.3, *p* < 0.58<br>*t* = 2.7, *p* < 0.01 | *F* = 2.3, *p* = 0.09<br>*t* = 0.8, *p* = 0.43 | *F* = 2.5, *p* < 0.01<br>*t* = 1.6, *p* = 0.12 | |

## Discussion

### *Birth date and individual litter size*

For practical reasons 1st April was used as birth date for cubs in this data set. The birth dates of most Danish red cubs are expected to be between 15th of March and the first week of April based on personal experience in the field and the birth date in relation to latitude (Lloyd & Englund, 1973). The birth weight of wild red foxes has been found to range between 80 and 130 g and as interpreted from reports on farmed silver foxes, cubs grow from a birth weight of around 100 g to 1kg in around four weeks (Tembrock, 1957; Lloyd, 1980; Hansen, 1991; Lassén et al., 2012). In this study the mean weight of young cubs between 23 days and 30 days i.e. within the nursing period was 1.3 ± 0.09S.E. kg (ranging from 800 g - 1.7 kg, n=13) (Figure 1). Moreover, the intercept of the regression lines for cubs less than 100 days of age was around 500 g (intercept: 0.585 and 0.526 for males and females respectively), confirming that most Danish fox cubs are born just before 1st April. Therefore, 1st April is considered to be an appropriate proxy for as a birth date for the present data.

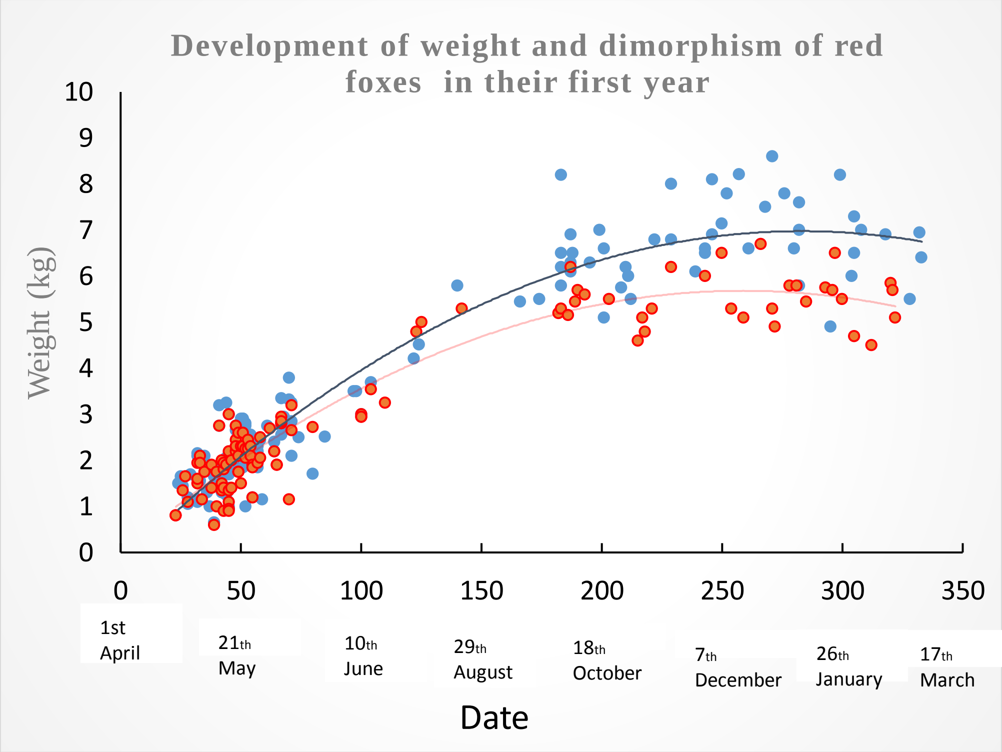

**Figure1.** Polynominal regression lines of weight (y) *versus* date/age of male (blue dots) and female (red dots) foxes within their first year. Considering 1st April to be the birth date of cubs, juvenile foxes will be around 50 days 21th May, 100 days 10th June, 150 days 29thAugust, 200 days 18th October, 250 days 7th December 300 days 26th January and around one year 17th March.

The onset of fecundity for foxes of both sexes is related to daylight, however, the time of birth of cubs show some variation, especially the onset of oestrus may be influenced by biotic factors (Lloyd & Englund, 1973). The birth date may be affected by the availability of food within areas of relatively close range (Kolb & Hewson, 1980b). In a study in North Dakota, almost all cubs caught at 207 dens were born between 15th March and 15th April (Sargeant et al., 1981). Also, Kolb & Hewson (1980a) found the date of conception, hence, the birth date of the cubs within a relatively close range (20-35 days). Although, these findings pertain to foxes in other parts of the world, they indicate that most fox cubs locally are born within a relatively limited period, most likely adapted to a period with optimal food resources to be utilised during the breeding season of the specific geographical area. The variance in the birth date of the wild foxes in this study may blur the dataset. However, since our model is based on 99 litters it is considered robust. Furthermore, the data noise due to different birth dates of litters will affect male and female age *versus* weight equally, and therefore not affect the development of SSD. As the 178 cubs originated from 99 litters, in average 1.8 cub (range 1-4) was caught from every litter, thus the size of individual litters i.e. "within litter" is not expected to influence the results.

### *SSD in cubs under 100 days of age*

We show that SSD in Danish fox cubs starts to develop around 100 days after birth (Figure 1). Our findings are in agreement with Storm (1976), who found no significant difference in the mean weight between male and female cubs from April through June (when cubs were less than 90 days old) in North American red foxes, but that SSD became significantly different between sub adults in September. Also, an illustration by Soulsbury et al. (2008) shows that SSD increases in juvenile British red foxes during the latter part of their first year

Lloyd (1980) found an 11% weight difference between British fox embryos of different sexes, corresponding to SSD of 3.4% (based on cubic root of body mass) in this early stage of life. Storm et al. (1966) found male cubs to be slightly larger and heavier than female cubs and referred to data where male foetuses in 17 out of 23 litters were on average heavier than those of females, and longer in 16 out of 23 litters, however that these differences were not significant.

Based on interpretation of data from Hansen (1991) and Lassén et al. (2012), the SSD of farmed silver foxes (*V.v. fulva*) show moderate sexual dimorphism from 2% to 4% in cubs within the first 100 days of life, increasing with age to around 5% to 6% around 220 days. Although farmed foxes have access to feed *ad libitum* and are 15% to 35% heavier than wild foxes, dimorphism increases with age. Nutrition may influence SSD, however, we assume that genetic components are predominantly responsible for the development of SSD.

Adult red foxes feed cubs from approximately one to three months of age, after which the cubs begin independent foraging (Baker et al., 1998). A lack of SSD in wild cubs within 100 days of life may therefor prevent male cubs from outcompeting females, i.e. prevent a skewed sexual ratio in favour of males from an early stage of life due to competition between smaller females and larger males when parents deliver prey.

### *Male biased SSD develops between independence of cubs and before mating*

The difference in growth rate between males and females is especially high during the period between 100 days of age and sexual maturity. The slope of the regression line age *versus* weight is almost twice as high for males than for females (slope of males =0.0219 and slope of females =0.0132). The more pronounced SSD before sexual maturity is probably due to the reproductive benefits of males and not for females having a lager body mass (Iossa et al. 2008). In a study of foxes in Bristol (UK), the body mass of males was found to be positively related to territory size, boundary pressure exerted on neighboring territories, and the number of litters sired both within and outside their resident group (Iossa *et al.* 2008). In contrast, life-history traits of females were not significantly related to body mass, suggesting that other factors are likely to affect female reproductive success (Iossa et al., 2008). In Danish red foxes, female fat reserves, but not body size was found to correlate with the number of embryos (Pagh et al., 2018).

### *Bimaturism or selection for larger foxes?*

The growth of both juvenile males and females levels of in the period between mating and one year of age. SSD in this period is slightly lower (6.9%) compared to the previous period (7.4%). The relatively lower body mass of male foxes in the breeding period is most probably due to high energy investment in reproduction. Several authors have reported changes in the body mass of both males and females during the mating and breeding seasons, especially males lose weight, whereas females may weigh more during the last period of gestation, and lose weight after parturition and in the period when they have to nurse and provide food for the cubs (Fairley, 1970, Lloyd, 1980a; Kolb & Hewson, 1980b; Hewson, 1984; Cavallini 1998).

Although individual foxes most likely stop growing at maturity, a study of Danish foxes showed that older foxes are heavier (Pagh et al. 2017). This is most probably be due to selection for larger foxes, although it cannot be ruled out, that foxes may grow after one year, or that older foxes are more experienced hunters (Iossa et al., 2008; Pagh et al., 2017).

It is unlikely that food-niche separation can explain sexual dimorphism in foxes; although adult males and juvenile foxes have been found to have a broader food-niche than adult females, their diets have a considerable overlap (Kidawa & Kowalczyk, 2011). It is more likely that selection forces favour larger male foxes, due to benefit from polygynous mating (Iossa et al., 2008).

### *Yearly variation in cub size*

In the present study, the growth rate of both male and female cubs showed significant variation from year to year, indicating that they become larger in certain years (Figure 2A, B, Table 2AB and 3A,B). Yearly variation in cohorts of foxes within the same area in relation to food supply has previously been found by e.g. Lindström (1983) and Sargeant (1978). Also, Soulsbury et al. (2008) argue that the yearly variation in body mass of adults is due to availability of nutrition between years. Soulsbury et al.(2008) found that rainfall (i.e. "worm nights") in July was related to juvenile development, and subsequently to the body mass of adult foxes. In at previous study of foxes in Denmark, SSD was found to range between 3.6 and 7.6 in adult foxes in periods with high and low density of foxes, respectively (Pagh et al., 2017). In periods with low density and minor competition for food among foxes especially male cubs may gain a larger body mass, thus increasing SSD in these periods. While Soulsbury et al. (2008) found that the fully grown foxes were affected by yearly environmental variation and nutrition, Sargeant (1978) and (Lindström 1983) found that foxes in North America and Sweden, respectively, compensated for periods of reduced growth with subsequent periods of rapid growth.

In the present study, the years 1966 and 1969 generally seem to be years of relatively higher growth rate and lower intercept for both males and females; in males, the slope of regression was higher in 1966 than in 1968, and in females the slope of 1966 was higher compared to all other years. The intercept of the regression line in 1966 was lower than in 1967, and in 1968 in males and females the intercept of 1966 was lower than it was in all other years (Figure 2A,B, Table 2A,B and 3A,B). Also, the slope and intercept of the regression lines for 1968 and 1969 differed significantly in males, the slope of 1969 being higher and the intercept lower than in 1968 (Figure 2A,B, Table 2A,A and 3A,B).

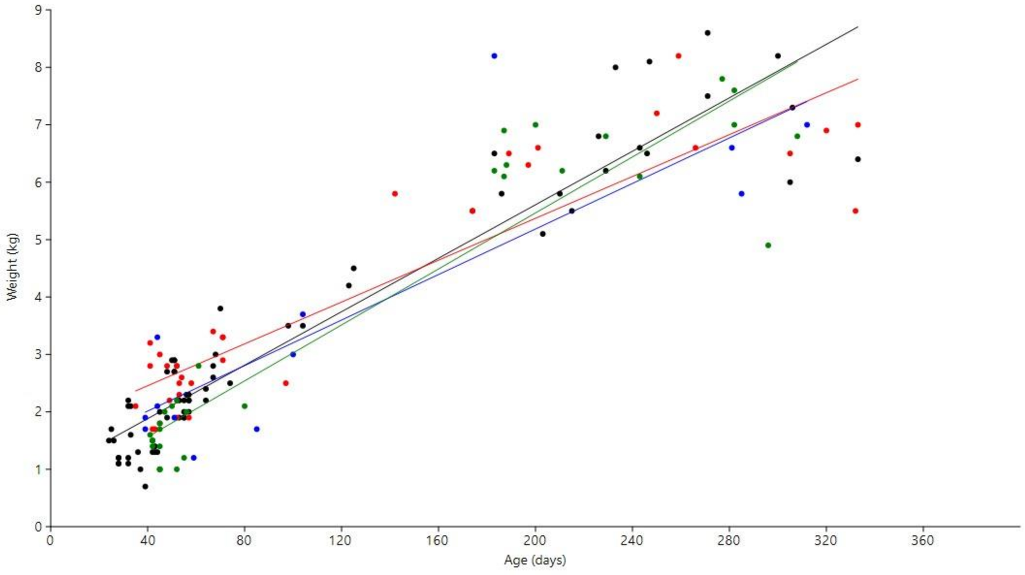

**Figure 2A.** Regression lines for age *versus* weight for males. Green line=year 1966, Blue line=1967, Red line=1968, Black line=1969.

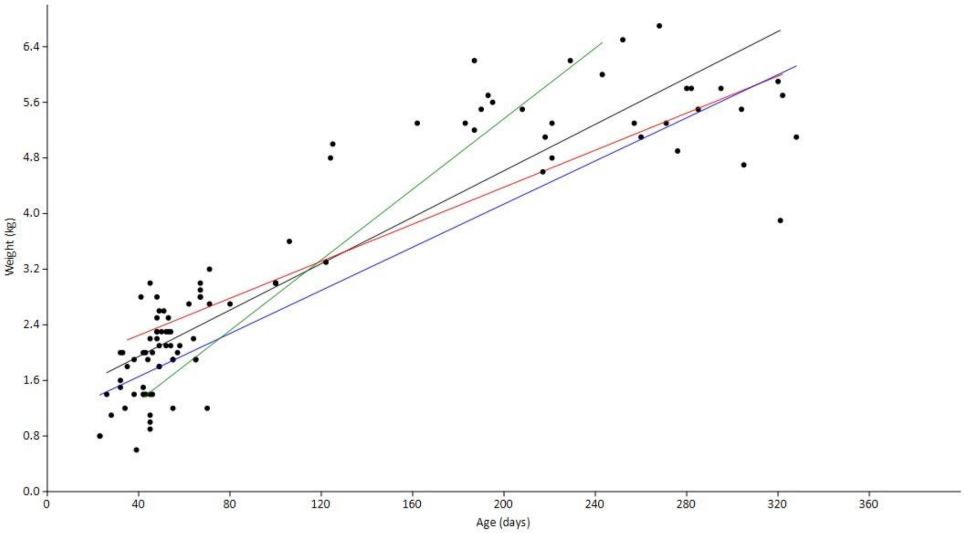

**Figure 2b.** Regression lines for age *versus* weight for females. Green line=year 1966, Blue line=1967, Red line=1968, Black line=1969.

At first hand, it may seem strange that there is a reverse relation between the numeric values of slope and intercept (figure 2A,B). However, the birth weight of cubs is smaller in years with large litter sizes (Lloyd 1980b). In years with low fox densities, hence more than average nutrition, litter size is found to be high (Voigt & Macdonald 1984; Heydon & Reynolds 2000; Goszczynski et al., 2008). Birth weight of cubs in years with plenty nutrition is expected to be smaller than average due to larger litter sizes. The ability to accelerate the weight gain in years with ample nutrition will favour the fecundity of females with large litters, even though cubs from these litters are smaller than average at birth.

Also, the body weights and SSD of adult foxes vary within years. A study of Danish foxes documented that adult males were significantly heavier (average weight between 7.5-7.7 kg) in periods of low population density compared to periods with high population density (6.8 kg) and that SSD ranged between 3.6 to 7.6 in adult foxes in high and low -density periods, respectively (Pagh et al. 2017). These differences in adult weights and SSD, may reflect yearly difference in growth of cubs.

## Acknowledgements

We dedicate this publication to Birger Jensen, who sadly passed away in December 2015. Birger was a great friend and naturalist, who provided invaluable knowledge about the biology of red foxes. Thanks also go to Christina Vedel-Smith, David Kjøller and Hans Viborg Kristensen (Natural History Museum of Aarhus) for providing access to museum collections no. 13000-13202, to Simon Bahrndorff for advice on figure illustrations and to Karin Coles for proofreading. We are grateful for the financial support from The 15th June Foundation and The Danish Nature Agency.

## Ethics approval and consent to participate

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. No ethical approval was required from an institutional or national ethics review board.

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