

Field report

Increased reproductive output of Danish red fox females following an outbreak of canine distemper



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Abstract

A decline in the Danish population of red foxes *Vulpes vulpes* due to an outbreak of canine distemper (CDV) in 2012 gave us the opportunity to test the hypothesis that the reproductive performance of foxes increases when the population density declines. The reproductive performance of 280 female foxes from two periods (mainly shot or road killed) in 1997-2000 and 2012-16, were compared. Game Bag Records of Jutland (GBRJ) were used as an estimate of population density. After a drop in GBRJ in 2013 due to the CDV epidemic, the mean litter size (based on dark placental scars from partum to oestrus) became significantly larger than in previous years; $F=4.3$, $p>0.03$, $H_c=8.1$, $p<0.02$. In 2015-2016, after population decline the mean litter size was $8.2 (\pm 2.5 \text{ SD})$ and in the breeding seasons before population decline in 1997-1999 and 2012-2013 the mean litter size was $5.6 (\pm 2.1 \text{ SD})$ and $5.7 (\pm 2.0 \text{ SD})$, respectively. During the period 1997-1999, barrenness was relatively high especially in yearlings, and the reproducing yearling foxes made up only 6% of the breeding females compared to 2012-13 and 2015-16 where breeding yearling females made up 53% and 61%, respectively. Age related differences in litter size and productivity were found in years with a relatively high population density, when older females in their third and fourth breeding seasons had the largest litter sizes and highest productivity. This was in contrast to the years with low population size, when no age-related reproduction was found, and when young females had relatively large litter sizes and high productivity. Rump fat thickness (RFT) of the breeding females was significantly higher in breeding females than in barren females, and the RFT was positively correlated to the number of embryos ($R^2=41\%$). This study confirms that the number of barren females drops, and the proportion of yearling females and litter size increase with reduced population density. Hence, culling or epidemics in fox populations increase production, most probably due to reduced competition among foxes, but will not change population size permanently. The present level of culling and traditional hunting in Denmark has no long-term effect on population size.

Introduction

The red fox *Vulpes vulpes* is a highly adaptable and relatively prolific species breeding once a year. In Denmark, the mating season starts in late December, and most cubs are born between 15 March and the first week of April after a 52-53 day gestation period (Lloyd and Englund 1973, Lloyd 1980). The mean litter size of foxes in Europe has been found to range between 3.3 to 6.9 cubs (Lloyd 1980, Cavallini and Santini 1996).

Several studies report a relationship between the reproductive performance in members of the family *Canidae* and population density. An association between high reproductive productivity (large litters and low proportion of barren females) on one hand and low population density on the other hand was documented by Heydon and Reynolds (2000a), comparing population recruitment and density between regions where a fox population had been reduced to different levels by culling. In Ontario, Voigt and Macdonald (1984) found low fox densities ($0.8/\text{km}^2$) and high litter size (mean=8.0), in contrast to Oxfordshire where fox densities were high ($2.15\text{-}10/\text{km}^2$) and

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litter size low (4-5 cubs). In Poland, the number of cubs per den decreased by 11% when fox densities increased after an anti-rabies vaccination period, which probably reflected an increased competition among foxes (Goszczyński et al. 2008). Also, studies of coyote *Canis latrans* populations show that an inverse relationship exists between population density and average litter size (Knowlton 1972), and packs of the rare Ethiopian wolf *C. simensis* produced larger litters during the recovery after a rabies outbreak (Marino et al. 2013).

A larger litter size, however, is not always the response to higher mortality in canid populations. Harris and Smith (1987) documented that foxes maintained productivity by reducing the proportion of non-breeding vixens in response to London fox control operations, rather than by altering litter size. Likewise, it was found in a more recent study of black-backed jackals *C. mesomelas* that the average litter size of females did not increase to compensate for higher mortality, but that it was compensated for by increasing the pregnancy rate and litter size of young individuals, thereby increasing the reproductive output (Minnie et al. 2016).

Food availability seems to be a key factor for the reproductive performance of foxes. For example, the number of barren females and litter size have been found to be adjusted to fluctuating numbers of prey in red foxes in Sweden (Englund 1970, Lindstrom 1988) and Arctic foxes *Vulpes lagopus* in Sweden (Angerbjörn et al. 1991) and Canada (MacPherson 1969). Angerbjörn et al. (1991) provided Arctic foxes with supplementary winter food and found an increase in the number of cubs per den the following breeding season. In Denmark, female foxes increase their body fat index during times of lower population density (Pagh et al. 2017).

Although scientific literature supports a relationship between fox densities and reproductive production, the effect of culling and game management and how fox population density regulates in relation to food supply is still discussed (Heydon and Reynolds 2000b, Gortázar et al. 2003, Baker et al. 2002, Baker et al. 2006, Baker et al. 2000, Baker and Harris 2006). Fox populations are known to recover fast after intensive culling campaigns or epidemics, and recovery may even exceed the effect of control measures (Bögel 1974, Rushton et al. 2006, Newsome et al. 2014, Lieury et al. 2015). Fox control is both controversial and time consuming, and studies on the effect of fox culling have given rise to different conclusions, e.g. Heydon and Reynolds (2000b) and Panek et al. (2006) conclude that culling can reduce fox numbers, while other studies conclude that human mediated regulation of foxes will not have long term effects on the population of foxes (Kolb and Hewson 1980, Hewson 1986, Kolb and Hewson 1980, Macdonald and Johnson 1996, Baker and Harris 1997, Baker et al. 2006, Baker et al. 2002, Baker and Harris 2006).

Fox control is widely used in small game management to improve the reproduction success of game species and hence increase the autumn yield of sport hunting (Beja et al. 2009). Many game managers view predator control as an essential tool to increase the income from hunting activities (Reynolds and Tapper 1996). Less than one century ago, predator control to the point of extermination was seen as a social duty, for the economic benefit of the community, and fox control has probably been practised throughout Europe since the first settlement of agricultural societies (Reynolds and Tapper 1996). More recently, interest has increased in the role of predators, and especially that of the red fox, in relation to declining populations of game species and of rare and endangered species in grass and wetlands.

Predator control and predator removal have also become an issue for conservationists (Bolton et al. 2007, Bolton et al. 2007, Fletcher et al. 2010). Ethical and biological arguments create demands for new approaches and restrictions to traditional wildlife management (Fall and Jackson (2002). Therefore, current governmental decisions to legitimize the control of predators rest not only on the benefit of game managers, but in a greater ecological perspective.

In Denmark, an outbreak of canine distemper (CDV) in the summer 2012 in the region of Jutland was reflected in a severe decline (30%) in the National Game Bag Records (NGBR) in the hunting season 2013/2014 (Trebbien et al. 2014, Asferg 2014, Asferg 2016). This population decline gave us a unique opportunity to assess the relationship between the reproductive performance of foxes and population density, assuming that annual variations in the GBR reflect changes in the population size. If the "turnover" of foxes (Lloyd et al. 1976) is density dependent, traditional culling will only change the demography of foxes and not the long-term population size.

The aim of this study is to test if the reproductive production of females increases when the fox-population (reflected by GBR) declines. We hypothesize that litter size and proportion of reproducing females increases when the fox population declines. Also we test if the body condition (expressed as Rump Fat Thickness, RFT) of female foxes is related to litter size, expecting a positive relationship between body fat index and litter size.

Methods

To test the hypotheses we compared changes in reproductive output of a total of 280 female foxes; 78 females before, 65 females during and 137 females after an outbreak of CDV. Foxes were sampled in different regions of Jutland in three sampling periods; before an epidemic of CDV in 1997-2000, during a CDV outbreak in 2012-2013, and after CDV and population decline during the winter of 2015/2016.

Litter size, productivity and barrenness are used as parameters for reproductive performance. Litter size was estimated from counts of placental scars (hereafter referred to as PSC) and embryos in the uterine horns. The carcasses of female foxes were stored at -20°C until examination. At necropsy, the uterus with ovaries and sections of jaws containing either the lower or upper canine tooth or the whole skull were removed. To find the PSC and embryos the uteri were thawed, and the uterine horns opened lengthwise. Canine teeth and skull were used for aging.

Litter size is given for reproducing females only, productivity as mean litter size including barren females. Females from 10-22 months of age were classified as yearlings (first breeding season females), whereas older females were classified as age-class 2, 3 and 4+ years. Females at least ten months old and with no reproductive activity, i.e. no PSC or embryos were characterized as barren. Females will on average be ten months old in February where embryos can be found.

Study area

Foxes were collected from primarily agricultural areas in Jutland, the Danish Cimbrian Peninsula covering an area of 29,775km, bordered to the south by Germany. The northernmost point of Jutland is located at 57°43'N/10°37'E. Denmark is characterized by flat, arable land and sandy coasts, low elevation and a mild coastal temperate climate. In the past three decades the climate in Denmark has changed towards higher winter temperatures and more precipitation (mainly rain). Mean winter temperature (December, January and February) from 1961 to 1990 was 0.5°C with a mean precipitation of 161mm. From 2006 to 2015 the mean winter temperature was 1.7°C, fluctuating between -1.5°C (2003) to 4.7°C (2007). The mean precipitation within the past ten years was 186mm, fluctuating between 319mm in 2007 and 107mm in 2009 (source: The Danish Meteorological Institute www.dmi.dk). In arable lands in Denmark, the foxes are opportunistic and the winter diet mainly consists of Microtine rodents, especially field vole *Microtus agrestis* and common vole *M. arvalis*, roe deer carrion *Capreolus capreolus*, birds, insects and fruit (Pagh et al. 2015).

Population changes during the study

The Game Bag Records are used as an estimate of population density. Especially during the summers 2012 and 2013, foxes were reported dead from all over Jutland, of which several were sent to the National Veterinary Institute, Technical University of Denmark and tested positive for CDV. CDV was recorded only in the region of Jutland (Trebbien et al. 2014, Asferg 2016), therefore the Game Bag Records of Jutland (GBRJ) were used as a relative measurement of population density (Figure 1). The distemper outbreak in Jutland began in 2012 and caused increased mortality in wild foxes in Jutland. The females (n=65) collected during the period 2012 and 2013 were part of a larger sample of 213 foxes (i.e. both females and males) from 2012-2013. All foxes were tested for CDV and only 3.5% tested positive (Albrechtsen et al. 2013). None of the 65 females from 2012-2013 had signs of CDV at necropsy. Typical signs of CDV are hyperkeratosis of the foot pads, purulent discharge and crusts around nose and eyes, and pneumonia, furthermore neurological signs can be seen. The disease is almost fatal within a short time after eruption, which occurs a maximum of eight weeks after infection. We therefore know that the females in our sample from 2012-2013 were not infected during the breeding season.

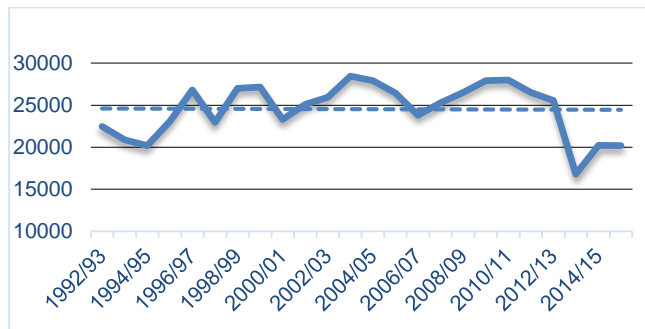


Figure 1. Game Bag Records of Jutland with tendency line during the two sampling periods. x and y denotes year and number of foxes respectively. Game bag records run from 1 April to 31 March the following year; however, most (80%) of the foxes will be shot from October to January.

In breeding seasons 1997-1999, the GBRJ was a slightly higher (mean=25,122 \pm 2,379 SD) compared to the previous five years (mean=22,673 \pm 2585 SD) (Figure 1). In the hunting season 2013/14, the GBRJ dropped by 38% (16,772 foxes) compared to mean hunting bags the previous five years (mean=26,837 \pm 1,134 SD.), the lowest record for 67 years. In the hunting seasons 2014/15 and 2015/16, game bag records had increased but were still 24% below average (Figure 1). Hunting and culling activities were assumed to be constant during the sampling periods. The average game bag record is defined as the mean game bag record five years before the sampling period.

In Denmark, the red fox has an open hunting season from 1 September to 31 January. Culling is allowed under certain conditions during the whole year. Culled individuals are included in the yearly game bag records for the hunting season which runs from 1 April to 31 March the following year. Approximately 80% of the foxes recorded in the game bag are shot in October-January, and most of the remaining 20% are culled during the summer as cubs (Asferg 2014).

Age determination

The age of the females, except for three females from 1997-2000, four females in 2012-2013 and 47 females in 2015-16, were aged from the number of annual growth lines visible in the tooth cementum in either the lower or upper canine. The foxes from 1997-2000 were analysed following Driscoll et al. (1985) and Ansonge (1995). The foxes from 2012-2016 were analysed according to Roulichová (2007). Both methods are considered as robust methods of aging foxes, and a comparison between dataset should not give rise to bias. Yearlings (first year breeders) are at least ten months old, born in the previous summer. Females between 0-10 months were determined juveniles, females from 10-22 months as yearlings and females in their second breeding season as 2+ [years] adults.

Foxes in different sampling periods

Carcasses of rural foxes in different regions of Jutland mainly shot by hunters or killed by cars were sampled in 1997-2000 (78 females; of these 40 juveniles, six yearlings, 29 2+ adults); in 2012-2013 (65 females; of these 24 juveniles, 19 yearlings, 19 2+ adults) and in 2014-2016 (137 females; of these 47 juveniles, 30 yearlings, 13 2+ adults). In the two later periods, foxes were collected as part of surveillance of wildlife diseases carried out by the National Veterinary Institute, Technical University of Denmark.

Female carcasses sampled between 1997 and 2000 originated from Mid-Jutland (74) and South-Jutland (4). Most were road kills (27), 25 were shot by hunters, 18 were found dead and eight died of unknown causes. The majority of the foxes sampled from 1997-2000 were killed from April to December (67%) and from January to March 24%. Females sampled in 2012-2016 originated from Mid-Jutland (108), South-Jutland (67), Northern Jutland (22) and five from unknown locations in Jutland. Most were shot by hunters (177), others were road kills (six), trapped (11), eight died of unknown causes. Females sampled from April to December were 62% and 56% from January to March.

Body size and fat reserves

To test if reproductive performance was related to the body size and condition of the female, fox carcasses not too damaged, skinned or decomposed were weighed to the nearest 100g, and a measuring tape was used to determine the length to the nearest centimetre from the tip of the nose to the last vertebra of the tail. For foxes from 2012-2016, the rump fat thickness (RFT; to the nearest millimetre) of subcutaneous fat around the pelvic girdle was measured in accordance with Prestrud and Nilssen (1992) and Prestrud and Pond (2003).

Reliability of placental scars counts and calibration of methods

Placental scars count (PSC) was used as an estimate for litter size, which is a widely used method. Dark scars represent live born or late abortions of cubs, while faded scars may represent resorption sites of embryos, or may have persisted from cubs born in a previous litter (Allen 1983, Lindström 1994, Cavallini and Santini 1996, Elmeros et al. 2003). However, the interpretation of scars as dark or faded and true litter size has been discussed by several authors (Englund 1970, Allen 1983, Lindström 1994, Elmeros et al. 2003).

The PSC in the uteri horns was counted and grouped as either dark or faded for the 2012-2016 samples. For the period 1997-2000, scars were classified in 1-6 grey shades then subsequently grouped as dark (shade 3-6) or faded (shade 1-2) following Lindström (1981) and Lindström (1994). When present, the numbers of embryos were counted. Scars were assigned as marks from a pregnancy from the previous breeding season, while embryos were assigned to the coming breeding season. Therefore scars from, e.g. January 2013 were included in the data as the breeding season 2012, while embryos from late January or February were assigned to the breeding season 2013.

The use of a grey scale (with six shades) to assess placental scars was introduced by Englund (1970). However, every study has used its own unique scale, and the evaluation of PSC is therefore, to some extent, subjective. To be able to compare scars from female foxes sampled in period 1997-2000 with those of 2012-2016, which were counted by different observers, dark and faded scars were calibrated between the observers using 12 uteri of which four were from farmed foxes with known litter size (Appendix 1). The calibration showed agreement between the number of live born cubs from farmed foxes, and PSC defined as dark by observers from period 2012-16 and PSC score/grey shade intensity 6-3 by observers from period 1997-2000. Furthermore, there was agreement between PSC defined as faded by observers from period 2012-16 and PSC score 2-1 evaluated by observers from period 1997-2000 (Appendix 1). Therefore, comparisons of litter size between the two sample periods were based on dark scars and embryos from female foxes in the time period 2012-16 and PSC scale 6-3 (from here on referred to as dark scars) and embryos from the period 1997-2000.

To test if dark and faded PSC differed between females collected in the period "partum to oestrus" (1 April to 31 December) and "oestrus to partum" (1 January to 31 March), the mean of dark and faded PSC from the two periods were compared (Appendix 2). As faded scars may also represent resorption sites of embryos, there may have been fewer resorptions in 2015-2016 than in 1997-1999 or more first year breeders meaning no faded scars from previous pregnancies. Correlating with the present study Lindström (1981) and Lindström (1994) found that scars fade throughout the year; during the period 2012-2016, a significant or close to significant drop was found between the mean number of dark and faded scars from "partum to oestrus" and "oestrus to partum". After oestrus, the uterus becomes swollen reducing the detectability of scars, and dark scars may fade, this may explain why the mean number of dark scars is higher before oestrus and that the mean number of faded scars is higher after oestrus. In 2012-2016, the mean number of dark scars was significantly lower in the period after oestrus than before oestrus, in contrast to faded scars being more prevalent after oestrus (Appendix 2).

Litter size and overall productivity between periods were therefore based on dark PSC from partum and oestrus. For the comparison of litter size and productivity among age classes, dark PSC from before and after oestrus and embryos were used.

To evaluate if litter size was related to the body condition of the females, RFT and the number of embryos was compared and the mean RFT of barren females and reproducing females was compared.

Data analysis

The software PAST was used for all the statistical analysis (Hammer et al. 2001). Differences in mean and median, of dark and faded PSC, between the periods “partum to oestrus” and “oestrus to partum”, the mean and median litter size, productivity and RFT between sampling periods, and the mean and median in RFT and body weight between sexually mature reproducing and non-reproducing females was tested using One-way ANOVA and Kruskal-Wallis tests respectively, when more than two samples were compared. A t-test and Mann-Whitney test were used for pairwise comparisons for the mentioned means and medians. A Chi-squared test was used to test the annual differences of barrenness in yearlings and all females more than one year of age, and the proportion of breeding yearling females in relation to the total number of breeding females. Linear regression and Pearson’s correlation coefficient were used to examine the degree of linear dependence of weight and RFT vs. the number of embryos.

Results

Table 1. Litter size (excluding barren), productivity (including barren), barrenness and proportion of breeding yearlings and all breeding females based. SD stands for standard deviation.

	<i>Breeding season 1997- 1999</i>	<i>Breeding season 2012 – 2013</i>	<i>Breeding season 2015 - 2016</i>	<i>Test</i>
Mean litter size of all females dark PSC partum to oestrus	5.6 (± 2.1 SD) N=14	5.7 (± 2.0 SD) N=13	8.2 (± 2.5 SD) N=12	F=4.3 p< 0.03 One-Way ANOVA: Hc=8.1 p<0.02, Kruskal-Wallis test Mann Whitney pairwise comparisons: 1997-1999< 2015/16, p<0.02 2012-13<2015-16, p<0.02
Mean litter size of yearlings – dark PSC partum to oestrus	N=0	3.6 (± 1.5 SD) N=3	7.6 (± 2.1 SD) N=7	Mann Whitney pairwise comparisons: 012/13<2015/16 t=2.8 p<0.03, z=2.3 p<0.02
Mean litter size of all females based on dark scars and embryos before and after oestrus	6.0 (± 2.2 SD) N=17	4.9 (± 2.2 SD) N=29	6.9 (± 2.2 SD) N=49	F=7.6 p< 0.001 One-Way ANOVA: Hc=13.3 p<0.002, Kruskal-Wallis test Mann Whitney pairwise comparisons: 2012-13<2015-16, p<0.003
Mean litter size of yearlings – based on dark scars and embryos before and after oestrus	6.0 N=1*	3.5 (± 1.4 SD) N=10	6.8 (± 2.0 SD) N=14	Mann Whitney pairwise comparisons: 012/13<2015/16 t=4.5 p<0.0002, z=3.7 p<0.0003
Percent barren yearlings	83% (5/6)	41% (7/19)	47% (14/30)	$\chi^2 =4$ df=2, p=0.14
Percent barren females (all females)	51% (18/35)	24% (9/38)	46% (42/91)	$\chi^2 =7$ df=2, p=0.03
Productivity of all breeding females-mean	2.7 N=35	3.6 N=38	4.3 N=91	
Proportion (and percent) of yearling females/ compared to females age two years and more	0.2 (15%) 6/29	1.1 (50%) 19/19	2.3 (69%) 30/13	
Percent breeding yearlings of all breeding females	6% 1/16	53% 10/19	61% 14/23	$\chi^2 =13$ df=2, p<0.002

*only one individual and not included in the test

Barrenness and productivity

Generally, barrenness was larger in yearlings; ranging from 41-83% compared to barrenness in all females including yearlings ranging from 24-51%. The number of barren females in general was significantly lower in the breeding seasons 2012-2013 (24%) than in 1997-2000 (51%) and in 2015-2016 (46%); $\chi^2 =8$ df=2, p<0.03 (Table 1). The proportion of yearlings in the sampled population in 1997-2000 was low (0.2, 15%), only six yearlings compared to 29 females from two to more than two years of age. This indicates a high mortality within the first year of the female’s life in 1997-1999.

Litter size before and after the outbreak of canine distemper

A significant difference in litter size was found before and after the drop in GBRJ due to CDV; F=4.3, p< 0.03, One-Way ANOVA Hc=8.1 p<0.02, Kruskal-Wallis (Table 1). The litter size (based on dark PSC between partum and oestrus) was significantly larger in the breeding season 2015 and 2016 (mean=8.2 \pm 2.5 SD) than in the breeding seasons 1997-1999 (mean=5.6 \pm 2.1 SD) and 2013 (mean=5.7 \pm 2.0 SD); p<0.02, Mann-Whitney pairwise comparisons (Table 1). Also, total counts of dark scars and embryos differed significantly between periods F=7.6, p<0.001, One-Way ANOVA and Hc=13.3, p<0.002 (Table 1). In yearlings, the difference in litter size was significantly higher as well in 2015-2016 than in 2012-2013; mean litter size of yearlings in 2015-2016 was 7.6 (± 2.1 SD) and in 2012-2013 the mean litter was 3.6 (± 1.5 SD); t=2.8 p<0.02, z=2.3 p<0.02 (Table 1). In 1997-1999 only one yearling female was breeding (Table 1).

In 2012-13 the proportion of yearling females to older females was 1.0 (50%), and in the period 2015-2016 the proportion was 2.3 (69%) (Table 1), indicating a proportional higher survival of young foxes in these periods. The percent of breeding yearlings in the population was significantly lower in the breeding seasons 1997-1999 (6%, only one individual) than in the years 2012-2013 (53%) and 2015-2016 (61%); $\chi^2 =13$ df=2, p<0.002 (Table 1). The productivity of females was 2.7 in 1997-1999, 3.6 in 2012-2013 and 4.3 in 2015-2016.

Age related reproduction

Age related difference in litter size was found only in the period 2012-2013, $H_c=9.3$ $p<0.03$ (Table 2). Pairwise comparisons revealed that the litter size of third year breeders was larger than that of yearlings (Table 2). Age related productivity was found in the period 1997-1999, $H_c=9.6$ $p<0.03$, productivity of females from four years and more was larger than that of younger females. Likewise, in 2012-2013, the productivity was larger in third year breeders compared to yearlings. In the years 2015–2016, no age-related litter size and productivity were found (Table 2). In the period 2015-2016 both litter size and the percent-breeding yearlings were relatively high compared to the previous periods.

Fat reserves in reproducing females compared to barren females

No significant difference was found between weight and length of breeding and barren females. However, breeding females had more fat reserves than barren females; the mean of RFT was found to be larger in reproducing females; mean RFT=0.77cm (± 0.33 SD, $n=48$) than in barren females; mean RFT=0.61cm (± 0.25 SD, $n=22$), $t=2.31$ $p<0.02$, $z=2.34$ $p<0.02$. Bivariate positive correlation was found between RFT and number of embryos in 11 females; $y=3.4x+3.7$, $R^2=0.41$, $t=2.5$ $p<0.04$, where x and y denotes RFT and no. of embryos respectively (Figure 2).

Table 2. Age-related litter size and productivity in relation to mean age of all females before and after oestrus.

Breeding season	Litter size (dark scars and embryos) 1997-2000	Litter size (dark scars and embryos) 2012-13	Litter size (dark scars and embryos) 2015-16
Yearling	6.0 (6) $n=1$	3.5 (1-5) $n=10$	6.8(4-12) $n=14$
Second	5.8 (4-6) $n=5$	6.0 (2-8) $n=4$	7.8(4-14) $n=5$
Third	7.5 (2-9) $n=2$	7.8 (6-10) $n=4$	6.3(6-7) $n=3$
Fourth +	5.8 (1-8) $n=8$	4 (4) $n=1$	10 $n=1$
Test Kruskal Wallis/ Mann Whitney	$H_c=0.85$ $p<0.84$	$H_c=9.3$ $p<0.03$ Pairwise comparisons $p<0.03$: Litter size of third season breeder larger than that of yearlings	$H_c=2.4$ $p=0.48$
Breeding season	Productivity (dark scars and embryos) 1997-1999	Productivity (dark scars and embryos) 2012-13	Productivity (dark scars and embryos) 2015-16
Yearling	1 $n=6$	2.1 $n=17$	3.2 $n=30$
Second	2.6 $n=11$	4.0 $n=6$	4.8 $n=8$
Third	2.1 $n=7$	6.2 $n=5$	4.8 $n=4$
Fourth +	5.8 $n=8$	2.0 $n=2$	10 $n=1$
Test Kruskal Wallis/ Mann Whitney	Kruskal Wallis $H_c=9.6$ $p<0.03$ Pairwise comparisons $p<0.03$ show that productivity of four years+ is larger than one year $p<0.01$, two years $p<0.04$ and three years $p<0.05$	$H_c=5.7$ $p=0.11$ Pairwise comparisons $p<0.03$: Productivity of third season breeder is larger than that of yearlings	$H_c=3.9$ $p=0.27$

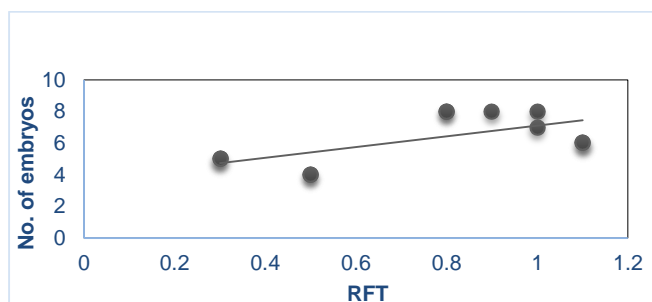


Figure 2. Relation between the number of embryos and rump fat thickness (RFT) in 11 females, $y=3.4x+3.7$, $R^2=0.41$, $t=2.5$. $p(\text{uncorr.})<0.04$, x and y denotes RFT in mm and no. of embryos respectively.

Discussion

Game bags as relative measure for population size

Although hunting game bags often are referred to as population measurements, game bag records may not provide reliable data for counting foxes or other animals (Baker et al. 2006, Kahlert et al. 2015). The number of

animals killed may depend on the effort expended by gamekeepers and hunters, and may reflect hunting behaviour and legislations at the current time (Baker et al. 2006, Kahlert et al. 2015). However, in this study the relative population drop is assessed from game bags within a period of five years previous to the three sampling periods to prevent bias caused by legislation and hunting behaviour. Hunting legislation did not change within these short periods and we assume that the hunting traditions have not change radically within five years. We therefore conclude that GBRJ can be used as a relative measure for population size in the sampling periods of this study.

Litter size in relation to body condition of females

After a rapid population decline due to CDV, the mean litter size of Danish foxes increased from around 5.6 (period 1997-1999) and 5.7 (2012-2013) to 8.2 (2015-2016) cubs after the outbreak of distemper. The litter size found in this study before the outbreak of CDV lies within the range for litter sizes reported in other studies carried out in Europe: Germany - mean=4.8(PSC) (Vos 1994), Italy - mean litter size= 3.9 (Cavallini and Santini 1996), Spain - mean =3.3 (PSC/embryo) (Zapata et al. 1998), Sweden - mean=3.6-6.0 (embryos) and 3.7-6.9 (PSC) (Englund 1970), England and Wales - mean=4.2-5.4 (embryos) (Lloyd 1980, Harris and Smith 1987), France - mean =4.7 (PSC) (Lieury et al. 2017). The mean litter size of Danish foxes after the outbreak of CDV is, to our knowledge, the highest recorded in Europe, but comparable to mean litter size found in Ontario, USA where Voigt and Macdonald (1984) recorded a mean litter size of 8.0 cubs in areas with low fox densities.

The mean RFT was significantly larger in reproducing females than in barren females, and the number of embryos correlated with RFT (Figure 2). In a previous study, Danish female foxes in the winters 2012-2014 had significantly lower RFT than females in the winters of 2015-2016, and male foxes were found to be almost 1kg heavier in the period 2015-2016 than males from 2012-14 (Pagh et al. 2017), suggesting that competition for food was lower in 2015-2016 than in 2012-14. McIlroy (2001) likewise found in a study of foxes in Australia that female foxes collected when the rainfall was above average contained significantly more *corpora lutea* (estimate of litter size) than females collected during the drought years, and suggest that drought reduces the availability of food. Allen (1983) found that body fat increased in relation to female age, and suggested that this could be an explanation for older females tending to have greater reproductive performance. The availability of food resources for foxes is likely to be important during the period when females need to accumulate fat reserves in preparation for breeding (Winstanley et al. (1999).

Barrenness in relation to population density

The percentage of barren females was relatively high in our study, ranging from 41% to 83% in yearlings, and from 24% to 51% in females in general, compared to other studies: in Germany, barren females comprised 15.3% of all females (Vos 1994); in Italy, 20% (Cavallini and Santini 1996); Spain, 13% (Zapata et al. 1997); Sweden, 11-79% (Englund 1970); and in England and Wales, 8.6-25.0% (Lloyd 1980, Harris 1979, Harris and Smith 1987). In Sweden, the proportion of barrenness in yearlings, particularly in northern Sweden, correlated negatively with food availability in the area Englund (1970).

Contrary to expected the proportion of barren females was lowest (24%) in 2012-2013 while the GBR of foxes was still relatively high (Table 1). The first response to mortality may be recruitment of more surplus females into reproduction indicating that CDV started earlier than officially recorded. This is in agreement with findings from our fieldwork where dead foxes were found already in spring 2012. In response to London fox control operations, Harris and Smith (1987) likewise found that foxes maintained productivity by reducing the proportion of barren females, rather than by altering litter size. Increased litter size may be a response to reduction in population size.

It is suggested that competition for food still existed between females during winters in the period 2012-13, as body fat (RFT) in adult females within this period was significant lower than in the winter 2015-16 (Pagh et al. 2017). The increase in barrenness in the period 2015-2016 most probably reflects that the population is increasing again after the drop in 2013 and 2014 (Figure 1).

In all sampling periods, barrenness was higher in yearlings than in females taken together. Yearling females have to find a breeding territory unless they stay in their natal territory. Hence, in dense populations, young females will have a disadvantage compared to older females, who already hold a territory, in contrast to periods with low population density and many vacant territories. Older females will in general have a higher body weight than yearling females (Pagh et al. 2017). Hence, older females may therefore have an advantage in agonistic fights. Cavallini and Santini (1996) found no relationship between barrenness and body size, which is in agreement with the present study.

Age-related reproduction

In this study, age-related differences in reproduction parameters were found in 1997-1999 and in 2012-2013, but not in 2015-2016, where yearling females were found to have a relatively high mean litter size (6.8, range: 4-12) (Table 2). Harris (1979), Kolb and Hewson (1980), Voigt and Macdonald (1984) and Harris and Smith (1987) found no age-related litter size in contrast to Allen (1983), McIlroy (2001) and Lieury et al. (2017) who found litter sizes to increase with age classes amongst younger age classes, peaking in 4-6 year females. In this study, the highest productivity of yearling females was seen in the years 2015-2016. Age-related reproduction may especially occur in dense populations where yearlings have to compete for resources with older females, while young females in low density populations develop faster in the food and territory rich environments and therefore have a high reproductive output in their first reproductive season (MacDonald et al. 1980, Cavallini and Santini 1996). The positive correlation between

RFT and the number of embryos found in this study (Figure 2) supports the hypothesis that a positive relationship between food availability and litter size exists, also found by McIlroy (2001). Culling and epidemics may reduce competition among females for territory and food, and increase breeding chances for yearling and surplus females and body fat and henceforward, litter size among the surviving foxes.

Winter climate, fluctuating prey and reproduction in the sampling period

Fluctuating numbers of voles in the diet of red foxes especially in the northern regions of Sweden influence the reproductive performance of foxes (Englund 1970, Lindstrom 1988). Extreme winter temperatures or precipitation may therefore theoretically influence prey availability of foxes in the sampling periods of this study. Fluctuations in the number of voles in Denmark occur, and significantly more voles were found in the stomachs of foxes in the winter 2012/2013, than in 2013/14 (Pagh et al. 2015), despite the fact that the winter 2012/13 was colder than the winter 2013/14 (mean temperature was 0.0°C and 3.7°C respectively (source: The Danish Meteorological Institute www.dmi.dk). Although it cannot be ruled out that unknown fluctuations in prey availability are responsible for the significant increase in reproduction in 2015-2016 (mean winter temperature 3.1°C), it is more likely that foxes compensate for minor yearly fluctuations in prey by switching to alternative, more available prey. This has occurred for prey species like brown hare *Lepus europaeus* decreasing from 7-3% in occurrence in the diet of Danish foxes, contrary to the occurrence of roe deer *Capreolus capreolus* increasing from 3-18% during the past 40-50 years, most probably reflecting population changes in the populations of brown hare and roe deer (Pagh et al. 2015). Hence, taking the generalistic and opportunistic diet habits of the fox and the generally mild winters in Denmark into consideration, it is likely that the population decline and the low density of foxes after CDV explains the significant increase in the reproductive output observed in 2015-2016 compared to previous years.

A study of body size of foxes in Denmark in different time periods indicates that foxes during the period 2012-2014 may compete for food resources, and that the body weight and size of male foxes and the body fat reserves of females are density dependent (Pagh et al. 2017). In this study, the body size of male foxes was generally smaller in the period 2012-2014 than in the period 1965-1977 where hunting pressure was high, and in the winter 2015/16 during the recovery from CDV (Pagh et al. 2017). This indicates that the Danish population of foxes at the present time outside epidemic periods is nearing capacity and competing for resources.

When does hunting regulate a fox population?

In areas where fox populations are stable from year to year, the annual productivity is equivalent to the total annual mortality, assuming that immigration into and emigration out of the area is equal (Lloyd et al. 1976). If mortality increases, productivity may be held constant by either increasing litter size or reducing the number of barren females in the population, or both (Lloyd et al. 1976).

Heydon and Reynolds (2000a) predict in their model "Demography of rural fox populations" how culling will affect a population: (1) Culling of a dense population with reproduction restricted by resources will result in an increased reproduction. (2) If the population is not limited by resources and reproduction not reduced due to competition for resources, culling will result in one of the following two possibilities: (2a) If culling is high relative to productivity, i.e. additive to mortality, culling will be an important determinant of fox density (2b) If culling is low compared to productivity and not additive to population mortality, then culling is not an important determinant of fox density. A study of the body size of foxes in Denmark revealed that male foxes after the population decline became larger and heavier, and that female foxes increased their body fat (Pagh et al. 2017), suggesting that there is competition between foxes in years without epidemics. Using the model by Heydon and Reynolds (2000a) therefore predicts that culling of foxes in Denmark will increase reproduction, which is in agreement with the results from this study.

Calculations by Lloyd et al. (1976) suggest that the annual turnover rate of a European fox population is about two-thirds i.e. more than 60%, based on a mean productivity per female of around 4.0 cubs. In this study, productivity ranged between 2.7 in 1997-1999 and 4.3 in 2015-2016. The ability to increase both litter size and the proportion of breeding females will result

in an even higher productivity. The high annual turnover rate in fox populations means that a significant proportion (more than 60%) of the population must be removed to result in a population decline, i.e. to obtain perceptible results in control campaigns (Lloyd et al. 1976). A productivity of 4.3 cubs per female in Danish foxes in 2015-2016 shows that mortality (including culling) in the Danish population has to exceed 60% before a population decline.

Concluding remarks

Our results document that the reproductive performance in red fox females quickly compensates for a declining population. Barrenness is relatively high in the Danish fox population, in comparison with other countries, meaning that the current hunting pressure on Danish foxes barely reduces competition for resources among foxes in periods without epidemics. This suggests that increased culling of foxes in Denmark will change the population demography to a larger proportion of young foxes, reduce the proportion of barren females and increase litter size most likely due to reduced competition among foxes, and therefore will have no effect on the total population size.

Ethical standards

The study complies with the current Danish laws. No animals were destroyed for the purposes of this study. The study was carried out as part of regular surveillance and monitoring of wildlife diseases by the National Veterinary Institute, Technical University of Denmark, Section for Diagnostics and Scientific Advice, Frederiksberg.

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Appendix 1

Results of calibration test for observer A and B. Observer A scored dark placental scars (PSC) as observer B scored PSC darkest grade 6-3 according to Lindström (1988), which was the number of scars equal to number of live born cubs from farmed foxes.

Fox	Month of death	Observer A				Observer B				Live born cubs	Remark
		PSC Dark	PSC Faded	PSC 6	PSC 5	PSC 4	PSC 3	PSC 2	PSC 1		
Farmed	Dec	4	2	0	4	0	0	0	2	4	
Farmed	Dec	4	0	0	0	3	1	0	(1)	4	
Farmed	Dec	4	0	0	3	1	1	0	1(2)	4	
Farmed	Dec	3	0	0	3	0	0	0	0	3	
Wild	Jan	0	6	-	-	-	-	-	-		Swollen
Wild	Feb	0	5	-	-	-	-	-	-		Swollen
Wild	Jan	(6)	-	(6)	-	-	-	-	-		Embryos
Wild	Nov	6	1	0	0	0	6	1	0		
Wild	Dec	4	4	0	0	4	0	0	2 (3)		
Wild	Dec	5	1	0	0	5	0	0	1		
Wild	Nov	9	1	0	0	0	8	0	(1)		

Appendix 2

Average litter size estimated from dark and faded scars and embryos in the periods “partum to oestrus” (1 April to 31 December) and that of “oestrus to partum” (1 January to 31 March).

Sample period N= no. of females examined in the period	Mean number of dark scars 6-3	Mean number of faded scars 2-1	Mean number of embryos
1997-2000			
Partum-oestrus	5.6 (n=14)	4.3(n=13)	0
Oestrus-Partum	8.3 (n=3)	4.5 (n=4)	0
T-test	t=2.2 p<0.05	t=0.1 p=0.89	
Mann Whitney- test	z=0.9 p=0.05	z=0.4 p=0.67	
2012-2013			
Partum-oestrus	5.7 (n=13)	1.6 (n=9)	
Oestrus-Partum 2	3.6(n=15)	2.3 (n=19)	6.0(n=4, 2013)
Test	t=2.9 p<0.01	t=1.9 p=0.07	
t-test	z=2.5 p<0.02	z=1.3 p=0.08	
Mann Whitney-test			
2015-2016			
Partum-oestrus	8.2 (12)	1.4 (7)	
Oestrus-Partum 2	5.9 (8)	2.6 (8)	6.6 (n=23, 2015) 7.0 (n=4, 2016)
Test	t=2.4 p=0.05	t=2.4 p<0.03	t=0.8 p<0.42
t-test	z=2.8 p<0.02	z=2.0 p<0.04	z=0.9 p<0.36
Mann-Whitney			