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Source: Folia Zoologica, 66(1) : 72-78

Published By: Institute of Vertebrate Biology, Czech Academy of Sciences

URL: https://doi.org/10.25225/fozo.v66.i1.a1.2017

Folia Zool. – 66 (1): 72–78 (2017)

Pre-, postnatal growth and maternal condition in a free ranging fallow deer population

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Received 2 December 2016; Accepted 10 March 2017

Abstract. We studied prenatal and postnatal growth rates and maternal effects in fallow deer (*Dama dama*) populations in free-ranging habitats in the Carpathian Basin. Data in this five-year long study were collected from pregnant females from December to the end of the hunting season (February), from newborns (May-June) and from 4-12 months-old fawns (October-June) in southwestern Hungary (Lábod region). The aims were to analyze foetal growth rate, assess the interaction between prenatal growth and maternal condition, and to examine factors influencing birth mass, and to measure fawn growth rates. During the study period foetal body mass (BM), body length (BL) and head length (HL) showed sigmoid growth. Correlations (r_p) among the three features (BM, BL and HL) ranged from 0.78 to 0.93. Foetal BM was a quadratic function of foetal BL in both sexes. Foetal BM was linearly and negatively related to maternal kidney-fat-index (KFI) and body mass. Average birth mass was greater in males (4.66 kg) than females (4.31 kg), and it was greater in the middle of the fawning season (in the middle of June) than in the beginning (in May). The BM and the KFI of the fawns decreased at the end of the winter (February, eight months of age) but increased thereafter. The growth analysis of fawns generally showed that males compared with the females were heavier and larger; however it was not manifested clearly in all cases.

Key words: *Dama dama*, gestation, foetus, fawn, growth analysis, maternal effects, Hungary

Introduction

Growth is basically influenced by genetic and environmental factors (Skogland 1985, Putman 1988, Clutton-Brock & Albon 1989). In cervids, maternal condition plays a determining role in prenatal growth (Putman 1988, Pélabon 1997), although other factors, such as age or food, also affect growth (Štěrba & Klusák 1984, Ahrens & Liess 1988, Náhlik & Sándor 2000, Sándor 2005). Early postnatal growth is influenced by the mother (nutritional condition, social rank), birth date, and fawn sex (Enright et al. 2000, Blanchard et al. 2004). Later growth is primarily determined by the individual genotype, sex, nutritional condition and social rank (Mitchell & Lincoln 1973, Clutton-Brock et al. 1984, Birgersson & Ekvall 1997, Pélabon 1997). The rutting season of the fallow deer (*Dama dama*) in Central Europe occurs mainly in October (Espmark & Brunner 1974, Sándor et al. 2014), and there is no embryonic diapause (Harrison & Hyett 1954, Siefke & Stubbe 2008). After fertilization, the ovum is implanted immediately, and development in the uterus and the growth of the embryo begin (Ahrens & Liess 1988, Siefke & Stubbe 2008). The gestation period lasts 33 weeks (225-237 days; Chapman & Chapman 1975, Bamberg 1985, Reinken et al. 1987).

Many factors can influence conception and prenatal growth, such as protracted rutting season (Ahrens & Liess 1988, Sándor et al. 2014), or the occurrence of the second rutting season in January (Siefke & Stubbe 2008), increasing conception, together with increasing heterogeneity of foetal body dimensions within a population. Birth date depends on growth of the cervid fawn (Clutton-Brock et al. 1982, Bienioschek et al. 1994). The majority of births in fallow deer take place from the middle of May to the end of June (Rieck 1955, Ahrens & Liess 1988). Later births appear to be disadvantaged, as later-born fawns are lighter (Pélabon 1997) and have higher mortality rates (Bienioschek et al. 1994) compared to early-born fawns. Male fawns have greater birth masses (Chapman & Chapman 1975, Bamberg 1985, Reinken et al. 1987, Pélabon 1997), although the literature data in birth masses according to sex are largely different (Siefke & Stubbe 2008), and the effect of other factors such as the population density on birth mass is also high (Morse & Miller 2009).

†*The study is dedicated to the memory of Kornél Ács (1978-2016)*

Numerous methods exist to estimate nutritional condition in ungulates (Kistner et al. 1980, Bookhout 1994). Among the simplest to measure *in vivo* are body mass and body size, with kidney-fat index, an index that can be measure; in harvested animals being strongly correlated to total body fat (Finger et al. 1981, Caughley & Sinclair 1994, Servello et al. 2005).

The aims of this study, conducted in a free-ranging fallow deer population, were 1) to analyze changes over time of foetal body mass and other metrics of foetal growth relationships; 2) to describe maternal effects on foetal growth, such as relationships of foetal body mass relationships to maternal body mass, kidney-fat-index and age; 3) to determine if birth mass and sex ratio depend on fawn sex and birth date, and 4) to assess sex-dependent changes of body mass and the kidney-fat-index in 4-12-month old fallow deer fawns. The main purpose of these investigations was to broaden knowledge about the reproduction of the fallow deer.

Material and Methods

Study area

The study area is located in the Pannonian biogeographical region of southwestern Hungary (Lábod region; centre: 46°11′ N, 17°30′ E; 164.6 km^2). It is basically a flat, lowland area with sand-dunes (mean 140 m, min. 107, max. 193 m a.s.l.). Forestry, wildlife management and crop cultivation are the region's most important sources of income. The vegetation consists of forests (53.5 %), one-third is English oak (*Quercus robur*), another one-third is willow (*Salix*), alder (*Alnus*) and linden (*Tilia*) species, and the rest is constituted mainly by locusts (*Robinia*). In two-thirds of the forested area, the age of the forests is under 40 years. In the arable areas, row crops, oilseed rape and cereals (36.7 %) are mainly cultivated, but pastures (7.5 %), fishponds and reeds (1.1 %), human settlements and orchards (1.2 %) also can be found. The climate is continental with some sub-Mediterranean features (e.g. moderately wet and relatively mild winter, balancing influences). The mean annual temperature is 10.3 °C, the average number of frost days is 87 days, the annual number of days with snow cover is 30-34, average snow depth is 6-10 cm, and mean annual precipitation is 740-760 mm (Dövényi 2010). The natural water supply of the area is favourable (Dövényi 2010) for the wildlife.

Intensive big game management has been practised in the study area, i.e. trophy hunting of fallow deer and red deer (*Cervus elaphus*), but the population of wild boar (*Sus scrofa*) is also important. On the hunting area of Lábod district of SEFAG Co., mean (± SE) harvest densities of 2.30 ± 0.42 fallow deer/km^2, 1.11 ± 0.08 red deer/km^2, and 1.93 ± 0.28/km^2 wild boar occurred during the study period. There are supplemental food plots and additional feeding in the area.

Data collection

Data were collected between 2010 and 2015 from fallow deer females (December-February), from newborns (May-June) and from 4-12-months old fawns (October-June). Considering the protracted rutting season (Ahrens & Liess 1988) and the detectability of foetal presence in the uterus (Harrison & Hyett 1954, Chapman & Chapman 1975, Ahrens & Liess 1988), gestation tests started in December, and finished in February, at the end of the hunting season. Foetal body mass (BM, n = 291) was measured within 1 gram, body length (BL) and head length (HL) was measured with caliper within 1 mm, and sexual differentiation was carried out on the basis of outer genital organ differences (Sándor 2005). The sex of the offspring can be recognized from the 10th week of gestation with macroscopic examination (Ahrens & Liess 1988).

The searching period for newborn fawns (n = 61) was based on actual field observation (K. Ács, pers. observ.). Professional hunters conducted strip searches every 1-2 days at potential fawning locations. Fawns older than one day are very difficult to capture (Siefke & Stubbe 2008). Fawn captures were made with long-handled nets (Mitchell & Lincoln 1973). Body mass (accurate to 0.1 kg), sex, and hoof condition (soft, light yellow foetal horn indicates birth within 24 hours) were documented.

Pregnant females were categorized into the following age groups: yearling (or primiparous) – 2 years old, young – 3-4 years old, middle-aged – 5-9 years old and old – over 9 years. Few (n = 15) females belonged to the old age group, so these are not included in the statistical assessment. Age estimation was based on the behaviour and physical features of individual before hunting, and using tooth emergence and replacement in young animals and tooth wear in older animals from harvested deer. Body mass after evisceration (body without inner organs, head and hooves) was measured within 1 kg for 4-12-month old fawns (males n = 239, females n = 295) and adult females (n = 291). Kidney fat mass was measured with digital libra within 1 g. The kidney fat index (KFI) calculation based on Riney's (1955) revised formula, i.e. KFI = (kidney weight plus perirenal fat weight) per kidney weight. The index value is presented as a ratio rather than a percentage.

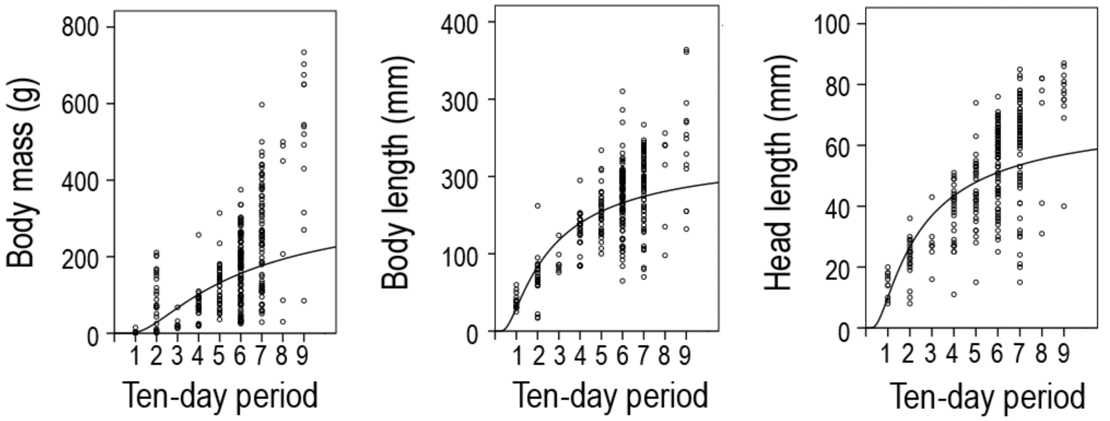

Fig. 1. Changes of the body mass, body length and head length of fallow deer foetuses between the first ten-day period of December and the last ten-day period of February (n = 291, Lábod, Hungary).

Statistical analysis

The foetal BM data between 1st December and 28th February were classified into nine ten-day long periods. During model selections (SPSS 11.5), models with highest R^2 and F values, and lowest standard error of the estimate (SE) were considered to best fit. The growth rates of individual foetal BM, BL and HL were regressed against time (i.e. ten-day period). The sigmoid model showed the best fit during the model selection. Relationships among foetal BM, BL and HL were analyzed with Pearson correlation. Foetal BL was regressed on individual foetal BM for each sex; quadratic model showed the best fit.

The relationship between KFI and BM of the pregnant females was analyzed with Pearson correlation. Regression analysis also was used to explore relationships between foetal BM and the KFI or BM of the pregnant females. During model selection, the linear model proved to be the best fit.

ANOVA (Bonferroni post-hoc test) was used to compare foetal BM, BL and HL data among maternal age groups (yearling, young and middle-aged) in each ten-day period. Independent t-test was used to explore differences in foetal BM, BL and HL between the sexes in each ten-day period.

Data on fawn birth date were classified into four periods: May (second half), and the three ten-day periods of June. MANOVA was used to analyze birth mass depending on sex and time within fawning season (Bonferroni post-hoc test, dependent variable: BM, fixed factors: sex, period). In the case of fawns, monthly mean value of BM and KFI were measured when males were 4-8-months old and females were 4-12-months old (different utilization

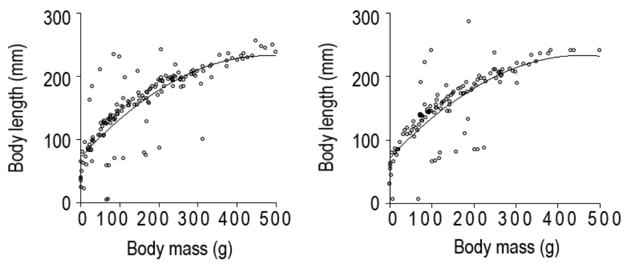

Fig. 2. The relationship between the body mass and body length of male and female fallow deer foetuses (n = 291, Lábod, Hungary).

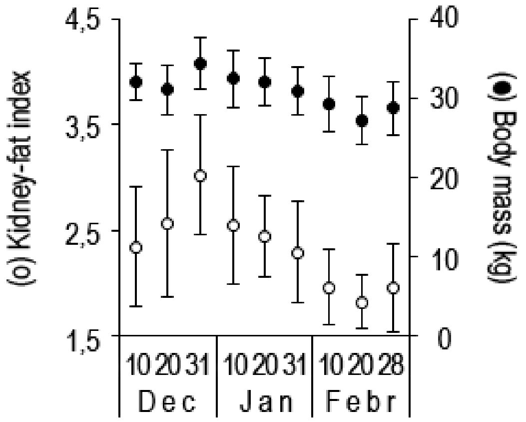

Fig. 3. Changes of the mean (± SD) kidney fat index and body mass of pregnant fallow deer females between the first ten-day period of December and the last ten-day period of February (n = 291, Lábod, Hungary).

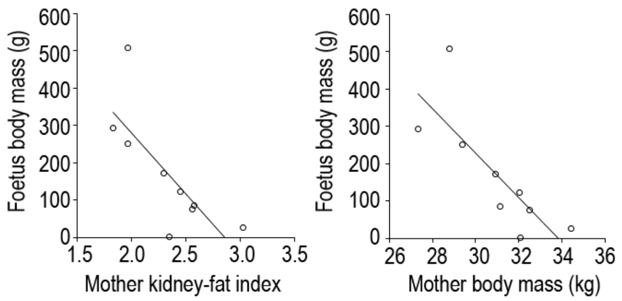

Fig. 4. Relationship between the mean kidney fat index and body mass of pregnant fallow deer females and the foetal body mass (nine ten-day periods, Lábod, Hungary).

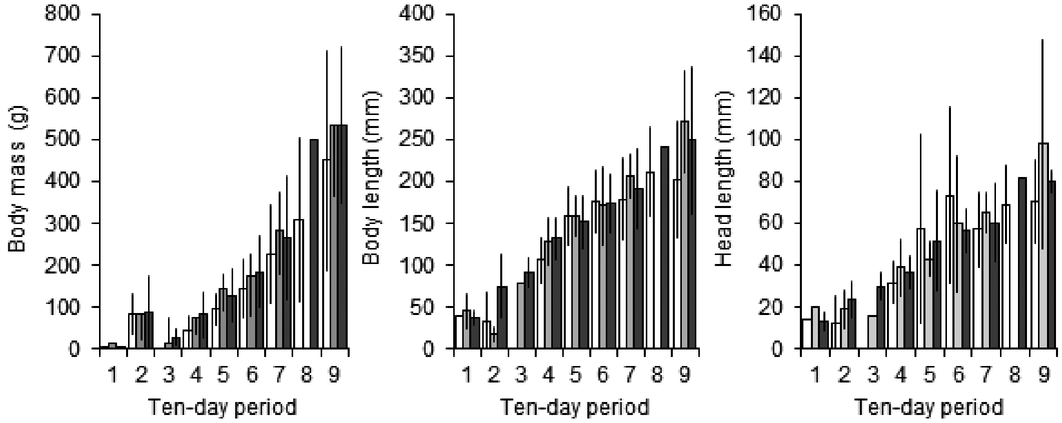

Fig. 5. Changes of the mean (± SD) body mass, body length and head length of fallow deer foetuses depending on age group of mothers, between the first ten-day period of December and the last ten-day period of February (n = 291, Lábod, Hungary). Yearling (2 years old) – white column, young (3-4 years old) – light gray column, middle-aged (5-9 years old) – dark grey column.

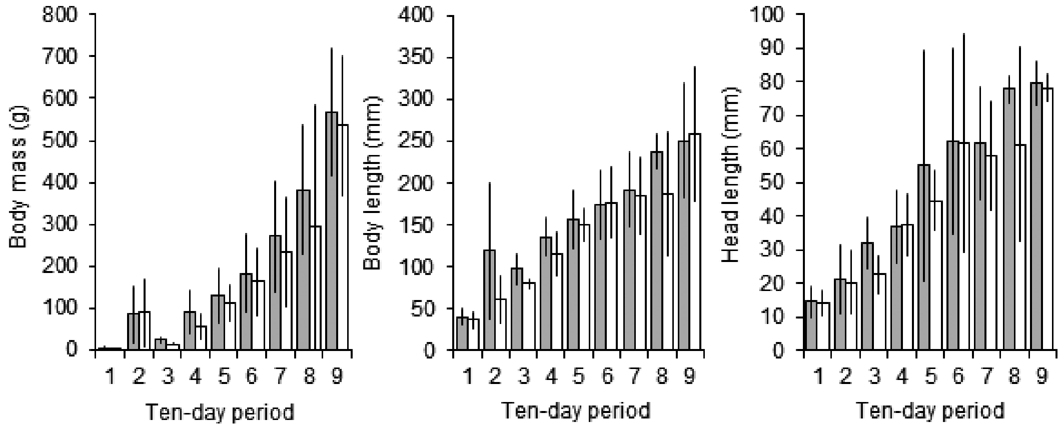

Fig. 6. Changes of the mean (± SD) body mass, body length and head length depending on the sex of fallow deer foetuses between first ten-day period of December and last ten-day period of February (n = 291, Lábod, Hungary). Males – grey column, females – white column.

of each sex). Independent-samples t-test was used to analyse differences between the sexes in each month (4-8-months old). Differences in KFI among periods by sex were tested with ANCOVA (dependent variable: KFI, fix factor: period, covariate: BM). The distribution of measured data was normal in each case. Sample size varied for analyses because of unmeasured features of some individuals.

Results

Foetal growth

The growth rate of foetal BM, BL and HL followed a sigmoid model over time (Fig. 1), moderating in the second half of the gestation period:

$y_{body\ mass}$ = exp (5.91 + –5.14/x) (R^2 = 0.54, SE = 0.84, F = 340.17, df = 1, 285, $P < 0.001$)

$y_{body\ length}$ = exp (5.46 + –2.06/x) (R^2 = 0.63, SE = 0.31, F = 484.90, df = 1, 284, $P < 0.001$)

$y_{head\ length}$ = exp (4.26 + –1.95/x) (R^2 = 0.52, SE = 0.33, F = 299.72, df = 1, 269, $P < 0.001$)

Correlation between foetal BM and BL was r_P = 0.781, ($P < 0.001$); between foetal BM and HL was r_P = 0.812, ($P < 0.001$) and between BL and HL was r_P = 0.926, ($P < 0.001$).

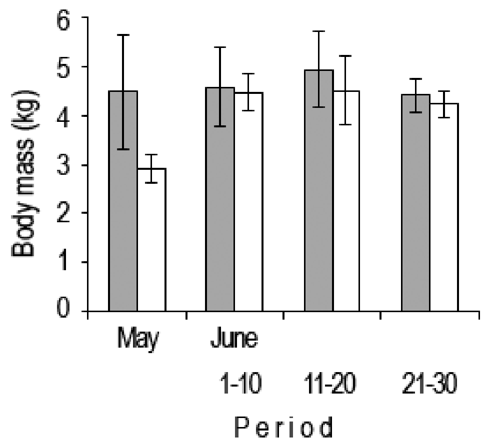

Fig. 7. Changes of the mean (± SD) birth mass depending on the sex of fallow deer fawns during the fawning season. Males (n = 32) – grey column, females (n = 29) – white column.

Table 1. Changes of the body mass and kidney fat index of fallow deer fawns depending on age, and the results of the statistical tests performed between males and females. Independent samples t-test was used to analyse differences between sexes.

Age (month)	Period	Male fawns			Female fawns			Statistical difference		
		Body mass (kg)								
		n	Mean	SD	n	Mean	SD	t	df	*P*
4	October	4	18.5	1.91	6	14.5	0.84	4.60	8	0.002
5	November	31	18.8	2.40	21	16.1	1.89	4.28	50	0.000
6	December	21	19.0	2.38	23	16.3	2.57	3.61	42	0.001
7	January	90	19.8	2.35	93	17.3	2.19	7.39	181	0.000
8	February	61	19.0	2.27	92	16.3	2.02	7.54	151	0.000
9	March				8	17.6	1.30			
10	April				3	18.7	0.58			
11	May				12	20.6	1.16			
12	June				8	23.1	1.25			
		Kidney-fat index								
4	October	4	1.65	0.287	6	1.81	0.157	1.13	8	0.290
5	November	30	1.70	0.363	21	1.81	0.340	1.12	49	0.268
6	December	21	2.11	0.587	23	1.94	0.505	1.09	42	0.284
7	January	90	1.88	0.363	93	1.91	0.429	0.40	181	0.687
8	February	61	1.50	0.334	92	1.47	0.281	0.57	151	0.573
9	March				8	1.20	0.114			
10	April				3	1.22	0.140			
11	May				12	1.41	0.149			
12	June				8	1.80	0.220			

Foetal BL was a quadratic function of foetal BM (Fig. 2), slowing noticeably after 250 g in each sex:

$y_{males} = 84.90 + 0.54x + 0.001x^2$ ($R^2 = 0.65$, SE = 34.82, F = 139.46, df = 2, 148, $P < 0.001$)

$y_{females} = 80.37 + 0.61x + 0.001x^2$ ($R^2 = 0.68$, SE = 33.92, F = 132.35, df = 2, 124, $P < 0.001$)

KFI and BM of pregnant females peaked at the end of December, then decreased until the middle of February before increasing again (Fig. 3). The correlation between the two features was $r_p = 0.417$, ($P < 0.001$).

Simultaneously, taking into account the data of foetal BM (Fig. 1) and BM and KFI data of pregnant females (Fig. 3) from each ten-day periods between December and February mean foetal BM was a negative, linear function of maternal KFI and maternal BM (Fig. 4), namely foetal BM increased as maternal BM and KFI decreased:

$y_{kidney\text{-}fat\text{-}index} = 929.60 - 324.92x$ ($R^2 = 0.58$, SE = 109.71, F = 9.87, df = 1, 7, $P = 0.016$)

$y_{body\ mass} = 2009.27 - 59.38x$ ($R^2 = 0.65$, SE = 101.15, F = 12.85, df = 1, 7, $P = 0.009$)

Mean foetal BM in yearlings was 16 % lighter (450 ± 260.7 g *vs*. 534 ± 164.1 g), BL was 23 % shorter (202 ± 68.8 mm *vs*. 261 ± 69.7 mm) and HL was 22 % shorter (70 ± 20.3 mm *vs*. 90 ± 36.5 mm) than the mean for adult at the end of the study period (Fig. 5). However, these differences among age groups were not significant for these characteristics (ANOVA, BM: F = 0.01-1.71, df = 1-2, *P* = 0.197-0.994, BL: F = 0.19-1.65, df = 2, *P* = 0.198-0.837, HL: F = 0.40-3.89, df = 1-2, *P* = 0.106-0.590). At the end of February (nine ten-day period), BM of male foetuses was 6 % greater than that of females (Fig. 6). The difference between the sexes in BL and HL was 2-3 % (Fig. 6). However, these differences were not significant (independent samples t-test, *P* = 0.056-0.932).

Fawn growth

Mean birth mass of males was significantly greater than that of females (4.66 ± 0.77 kg *vs.* 4.31 ± 0.65 kg, MANOVA, F = 6.98, df = 1, *P* = 0.011), and significantly greater in the middle of the fawning season than at the beginning (F = 3.39, df = 3, *P* = 0.025, Fig. 7). The sex × period interaction was not significant (F = 1.49, df = 3, *P* = 0.227).

KFI of yearlings increased from October to December, then decreased in January and February (Table 1). In male fawns, the KFI was lowest in February (ANCOVA, F = 13.55, df = 4, *P* < 0.001). The KFI of female fawns continued to decline, with a nadir in

March-April (ANCOVA, F = 17.89, df = 8, $P < 0.001$), before increasing in May and June. KFIs did not differ significantly between the sexes in the five months of comparisons (Table 1). BM of both sexes slightly decreased in February (8-month old), then began increasing again. BM of males was significantly greater than the females from October to February (Table 1).

Discussion

Sigmoid models provided the best model fit for growth of fallow deer foetuses. Within the study period, variation in conception dates (Harrison & Hyett 1954, Chapman & Chapman 1975, Ahrens & Liess 1988, Dye et al. 2012, Sándor et al. 2014) contributes to wide individual variation, and because of this, variation in foetal development also was related to the date of data collection (i.e. consideration of the pregnancy detection time) from hunted samples. According to Ahrens & Liess (1988), 14 % of all females were fertilized before 20th October, but most of females (38 %) were fertilized after 1st November, during the post-breeding season. The reason could be that the earlier fertilization was unsuccessful or the embryos died in an early foetal stage. This study confirmed Ahrens & Liess (1987), who observed that the BL of a two-week old embryo reaches 5 cm in mid-December. After that, foetal growth rate increased highly and BL reached 20 cm length at the end of the hunting season, as it was revealed in earlier studies (Harrison & Hyett 1954, Chapman & Chapman 1975, Ahrens & Liess 1988). According to the present study, there were strong relationships among BM, BL and HL of foetuses. These relationships (correlation, quadratic model) suggest that BM or BL provide information about foetal growth.

Foetal BM increased linearly as maternal BM and KFI decreased. Foetal BM, BL, and HL of yearling mothers tended to smaller values compared to foetuses of older mothers. We considered these differences to be biologically important. The lack of statistical support came from the high standard deviation values in each ten-day period, which can be linked to the wide variation in the time of conception detailed above (Štěrba & Klusák 1984, Ahrens & Liess 1988, Putman 1988, Náhlik & Sándor 2000, Sándor et al. 2014). Fawns of older mothers are generally larger at fawning and also at weaning (Bienioschek et al. 1994).

During the study period, the sex difference in the foetal growths were not significant, while in other studies (Birgersson & Ekvall 1997, Sándor 2005) the BM and BL growths at males were higher than females. Fawns in our study area had greater BM than in some other areas, e.g. Pélabon (1997) in France (in captivity; males: 3.89 kg, females: 3.18 kg, n = 79) and Bamberg (1985) in Germany (4.44 kg *vs*. 4.28 kg, n = 35), but were similar to masses reported by Chapman & Chapman (1975) in Britain (4.60 kg *vs*. 4.40 kg, n = 93).

We found that 90 % of all births occurred in June (41 % in the middle ten-day period of June), which was similar to previsous work. According to Rieck (1955), in Germany, 12 % of all births had happened in May, 72 % in June and 16 % in July. Ahrens & Liess (1988), on the basis of developmental status of embryos, calculated that most births (77 %) occurred between 21th May and 20th June, and most of them in the first 10 days of June. Birth masses in our study were higher in the mid-fawning period in June than in the beginning (May). This contrasts with the results of Birgersson & Ekvall (1997), who recorded greater masses at fawns at the beginning of the fawning period. Earlier birth dates allow fawns to nurse for a longer time (Birgersson & Ekvall 1997), which eventuates faster growth and greater weaning BM (Bienioschek et al. 1994, Siefke & Stubbe 2008). According to Putman (2003), the mass of fawns that were born on the first week of June were significantly higher at the beginning of winter than those that were born later. The slightly decreasing BM of fawns at the end of winter (males) or beginning of spring (females) was similar to earlier studies (Bienioschek et al. 1994).

BM of male fawns was higher than the female ones at the birth and at the 4-8-month old age group, whereas KFI showed less difference between the sexes. Bienioschek et al. (1994) also found that the BM growth rate of male fawns was higher than females in free-ranging and farmed populations.

In conclusion, the mother's investment to the offspring is demonstrated by the negative relationship between maternal condition (BM and KFI) and the BM of foetus. Further studies are needed to determine if the winter period or other factors may have caused a decline condition of fallow deer mothers during winter. The growth analysis of fawns generally shows that males are heavier and larger, along with more maternal investment compared with the females; however it was not manifested clearly in all cases. Knowledge of growth models based on data collected from free ranging fallow deer populations may give basis for comparisons among years or areas, which may give a better understanding of reproduction.

Acknowledgements

Thanks to S. Csányi, E.C. Hellgren, N. Nagyapáti and anonymous referee for helpful advice and comments on early draft of the manuscript.

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