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SHORT COMMUNICATION

I can produce more offspring as you can imagine: first records on exceptionally large litters in roe deer in central/southern Europe

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Abstract Most roe deer females produce twins and more rarely singletons and triplets. Some very rare reported cases of litters above three offspring refer to quadruplets which are, however, very much an exception in roe deer reproduction (only some tens of documented cases can be found in the scientific literature). In this paper, we present the first firm evidence that roe deer females are able to produce even five offspring. By examination of large sample set (n = 4690) of roe deer uteri and ovaries in two neighbouring countries in southern/central Europe (Italy and Slovenia), we found ten females that either carried or had potential to produce quadruplets, and in three does the (potential) litter size was even five. While one doe from Slovenia had five corpora lutea, two does from Tuscany, Italy, carried five foetuses. In both cases, all foetuses were normally and equally developed, indicating that none of them had predominant exposure to resorption/abortion. Six out of 13 females with exceptionally large potential litters (>3 offspring) had significantly higher body mass in comparison with mean body mass of all does harvested in the same hunting management district and in the same period, while five of them were significantly lighter. This indicates that some roe deer females can produce exceptionally large litters even when their phenotypic quality is not higher than the average in the population, and that such large litters are a stochastic episode rather than a reproductive performance of a very vital individual(s).

Keywords Roe deer · Litter size · Exceptionally large litters · Offspring · Foetus · Corpora lutea

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Introduction

European roe deer (*Capreolus capreolus*) is the most widespread and abundant European wild ungulate which has shown marked increase in population size for decades (see Andersen et al. 1998a; Apollonio et al. 2010). One of the main factors enabling fast population growth is high reproductive potential of this polytocus species (reviewed in Flajšman et al. 2013). Contrary to other native continental European ruminants in which females generally start to reproduce at older ages and normally produce only one offspring per pregnancy (e.g. red deer (*Cervus elaphus*): Clutton-Brock et al. 1982; Borowik et al. 2016; moose (*Alces alces*): Garel et al. 2009; Gingras et al. 2014; European bison (*Bison bonasus*): Krasiński and Raczyński 1967; Alpine chamois (*Rupicapra rupicapra*): Schröder 1971; Pyrenean chamois (*Rupicapra pyrenaica*): Pérez-Barbería et al. 1998; Alpine ibex (*Capra ibex*): Garnier et al. 2016), most roe deer does produce twins and more rarely singletons while triplets are also quite common (Danilkin 1996; Andersen et al. 1998b). For example, in early studies on the reproductive performance of roe deer females, the reported proportions of does carrying more than

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one embryo were between 60.9% (Switzerland) and 87.0% (Denmark), and triplets were found in between 4.3% (Denmark) and 31.9% (Sweden) of analysed does (reviewed in Krže 2000). Usually, triplets are more common in Scandinavia, and northern populations have larger litters than southern ones (Andersen et al. 1998a; Andersen and Linnell 2000).

In roe deer, all reported cases of litters above three offspring, either found on the basis of counting embryos/foetuses or corpora lutea, refer to quadruplets which are, however, very much an exception in roe deer reproduction (Danilkin 1996). According to the review, provided by Stubbe et al. (1982), the highest frequency (6.4%) of quadruplets was reported in Sweden (3 cases out of 47 analysed does); 5.6% of quadruplets (4/72) were found in Hungary; 3.4% (7/206) in Lithuania; 1.9% (1/54) in England; 1.1% (4/362) in another study in Sweden; and 1.3% (1/73), 0.3% (2/573) and 0.2% (1/438) in three different areas of Switzerland, respectively. More recent report on females with four embryos was from Belgium (Wauters et al. 1995). In two countries where data for this paper were collected, existence of four offspring in roe deer has not been evidenced in the literature so far (Italy), while in Slovenia there is a one firm evidence of quadruplets, dated in 1952, when a feral dog killed a doe with four foetuses, two males and two females (Flajšman et al. 2014a).

A very few reports on larger (>3) litters in roe deer might be due to the relatively small sample sets in the majority of studies on reproductive potential of the species (see Flajšman et al. 2013), and consequent high possibility that such indeed very rare cases have been rather overlooked. Therefore, we combined data on examination of roe deer uteri and ovaries from two very recent independent studies, operated with a very large sample sets (4690 adequate samples in total) in two neighbouring countries in southern/central Europe (Italy and Slovenia). We aimed to (i) determine the occurrence and frequency of the exceptionally large potential litters (for the purposes of this paper, we understand every female carrying >3 embryos/foetuses or corpora lutea as an exceptional breeder which had a potential to produce >3 offspring); (ii) compare body mass, which is in roe deer as an income breeder particularly informative proxy of individual condition and quality (e.g. Andersen et al. 2000) and determines reproductive performance of females (e.g. Gaillard et al. 1992; Hewison 1996; Hewison and Gaillard 2001; Hamel et al. 2009; Flajšman et al. 2014b; reviewed in Flajšman et al. 2013), of mothers carrying >3 corpora lutea or foetuses with the average for all does that were harvested in the same periods and in the same regions. We hypothesised that exceptionally large litters are produced only by does with remarkable phenotypic quality, i.e. those whose body mass substantially exceeds the average body mass of comparable females shot in the same area/period.

Material and methods

Study areas and sampling

In Italy, sampling of reproductive organs of roe deer females (uteri with ovaries) was made in 1360 hunting grounds (mean size: 109.35 ha ± 1.22 S.D.), distributed in 22 hunting management districts (HMD) in the Arezzo province (Tuscany, Central Italy, 3235 km^2). The average size of studied HMD was 9490 ha, and they cover the whole gradient of environmental conditions and population characteristics of the species distribution in the Apennine area. In total, 4124 samples were collected, and 3110 of them (410 yearlings, 2649 adults, 51 with unknown age) were suitable for the analysis considering the scope of this paper (samples with both ovaries and/or intact uteri with foetuses). All samples were collected within the regular hunting operations in hunting season on roe deer females in this part of Italy, from 1 January to 15 March (2006–2015: n = 2960, of which 2861 with both ovaries and 2816 with intact uteri), and from 1 August to 18 September (2007–2008: n = 1145; however, to exclude the risk that in this subset some uteri would be from the pre-rut period we used samples from September only: n = 150).

In Slovenia, sampling of reproductive organs of roe deer females was made in 85 hunting grounds (mean size: 6908 ha), distributed in 14 (out of 15) HMD, covering the whole gradient of environmental conditions and population characteristics of the species distribution in the country (20,273 km^2). In total, 1896 samples were collected and 1580 of them (333 yearlings, 1184 adults, 63 with unknown age) were suitable for the analysis considering the scope of this paper. The majority of samples were collected within the regular hunting operations in hunting season on roe deer females in Slovenia, from 1 September to 31 December (2013–2015: n = 1545), and some samples were collected also from road-killed does in the period 1 January–30 June (2014–2016: n = 35).

Treatment and analyses of uteri/ovaries

Immediately after the cull and dissection, hunters placed uteri into plastic bags and stored them frozen until collection. For each specimen, sampling date, location, eviscerated carcass mass (total body mass less viscera but with head and feet on) and age group (yearling, adult) were recorded in each hunting ground in both countries. Afterwards, samples were defrosted and analysed in the laboratory of Casa Stabbi field station (Italian samples), at the institute ERICo Velenje or at the Slovenian Forestry Institute (Slovene samples). To

determine the potential litter size, the number of corpora lutea (CL) was counted after the dissection of each ovary (for does, harvested in the September–December period); in the case of their presence, also the number, gender, size and weight of foetuses (F) were determined (winter harvest and spring road-kill). Although the actual litter size may differ from the potential one (determined on the basis of CL/F counts) due to implantation failure, abortions or neonatal mortality we considered data on the number of CL/F as an adequate indicator of the potential of roe deer females to produce a given number of offspring since (i) in healthy adults, which are expected to be the only ones that are able to produce exceptionally large litters, losses due to resorption of foetuses are minimal, generally in the order of 1–4% (Danilkin 1996); (ii) in prime-age does, which are primarily expected to have potential for producing larger litters due to their higher body mass (Flajšman et al. 2017), implantation failure is much lower than in primiparous and senescent ones (Hewison and Gaillard 2001), and is usually <10% (Borg 1970; Strandgaard 1972) which was confirmed also by our data (see "Results and discussion" section).

Age determination/assessment

In both countries, mandibles of all studied individuals were also collected during regular hunting procedure, and age was assessed by macroscopic inspection of tooth development and tooth wear (e.g. Ratcliffe and Mayle 1992). Due to the known uncertainty in the age assessment of adult roe deer on the basis of tooth wear criteria (see Hewison et al. 1999), the age of adults was not determined with a yearly precision. Rather, animals were grouped into the following age categories: yearlings (15–19 months old), 2-year-olds, young adults (3–4 years), middle-aged adults (5–7 years), old adults (8–9 years) and senescent adults (10+ years), respectively. In Slovenian subset, age assessment was made in consensus of both Slovene co-authors of the manuscript (their separate pre-assessments differed in <5% of all mandibles), and pre-prepared set of mandibles with easily distinguished tooth wear patterns was used as a criterion for classification. In an Italian subset, the macroscopic assessment of the age was validated by histological examination of teeth, i.e. by counting annual cementum layers in sample set of >300 individuals (see Capitani et al. 2005).

Comparison of exceptional breeders with other females

For comparison of body mass of does carrying four or five CL (or F) with other relevant does we employed data on every single adult female (no yearling had >3 CL or >3 F, therefore they were excluded from this analysis), harvested in the same month of the relevant year and in the same HMD as any exceptional breeding doe. For Italian samples, those data were adopted from the Arezzo Province dataset and for Slovenian ones from the on-line available Slovene hunting information system (Lisjak 2016). In both databases, several data (including body mass) on every single harvested ungulate must be registered by responsible wildlife managers. Data on mean body mass of compared individuals and parameters of statistical tests are presented in Tables 1 and 2. For comparison between exceptional breeders and other does, parametric statistics (t test) with the limit of statistical significance set at $p < 0.05$ was performed by STATISTICA (data analysis software system) (StatSoft 2014).

Results and discussion

Irrespective of age, the majority of roe deer females sampled in the period 1 September 2013–30 June 2016 throughout Slovenia (n = 1580) carried two (73.5%), followed by one (19.8%) and three CL (3.7%). Five adults (0.4%) carried four, and in one (0.1%) we found even five CL. The majority of does sampled in the period 1–18 September 2007–2008 throughout Arezzo Province (n = 150) carried two (61.9%), followed by one (24.5%) and three CL (4.8%). Also, when analysing the winter hunting data (1 January–15 March 2006–2015; n = 2960), the majority of females carried two foetuses/CL (F: 68.7%; CL: 77.2%), followed by one (F: 18.3%; CL: 7.5%) and three (F: 7.2%; CL: 10.5%), respectively. Four adult does (0.2%) carried four, and in two (0.1%) we found even five foetuses (Fig. S1); all those six does carried four CL. Data on all roe deer females with potential litter size >3 are presented in Table 1 (for Slovenia) and Table 2 (for Arezzo Province), and detailed frequencies of the number of CL/F per yearlings/adults are provided in the Supplementary material (Table S1).

Exceptional breeders with the ability to carry more than three offspring were present in a low frequency (0.5% in Slovenia, 0.3% in Italy) which confirms that larger litters are very much an exception in roe deer reproduction (Danilkin 1996). Nevertheless, also in central/southern Europe, some does obviously have the ability to produce more offspring: we found ten cases of does that either produced quadruplets or carried four CL, and in three cases the (potential) litter size was even five. To the best of our knowledge, this represents the first firm evidence that roe deer females are able to produce even five offspring which was evidenced both by counting of CL (in Slovenia: one case) as well as by the presence of foetuses (in Italy: two cases). Although the number of CL and/or foetuses does not necessarily reflect the actual litter size either due to the implantation failure of the fertilized blastocyst(s) in mid-winter or resorption of the embryo(s) during pregnancy, previous studies showed that implantation failure is higher among primiparous and senescent does while it is relatively low in prime-age ones (e.g. Hewison and Gaillard 2001) in

Table 1 Data on roe deer females with potential litter size >3, harvested in Slovenia in the period 1 September 2013–31 December 2015, accompanied by data on mean body mass of all adult females, harvested in the same year/month and in the same hunting management district (source: Lisjak 2016)

ID of doe[a]	District[b]	Hunting ground (code)	Location (quadrant)[c]	Gauss-Krüger coordinates (X,Y)[d]	Date of cull	Body mass (kg)[e]	Age (years)	CL (*N*) (L+R)[f]	Mean body mass (kg) of does in the district[g]		
									Mean ± 1.96*SE (min–max)	*N*	*P* value
79	II	Jesenice (203)	G3L3	433500 143500	16 Sep 2013	13.0	5–7	5 (3+2)	14.9 ± 0.2 (10.0–19.5)	228	<0.0001
118	IX	Šentjur (922)	P7I8	527500 118500	14 Sep 2013	15.0	3–4	4 (3+1)	15.2 ± 0.2 (8.5–21.0)	257	0.1981 (ns)
487	IX	Oljka (902)	N0K3	500500 133500	6 Sep 2014	16.5	5–7	4 (3+1)	15.3 ± 0.3 (8.5–22.0)	279	<0.0001
540	VI	Hoče (632)	R9M2	549500 152500	27 Sep 2014	20.5	8–9	4 (3+1)	14.9 ± 0.3 (8.0–20.5)	218	<0.0001
1538	VIII	LPN Fazan (829)	W7M5	597500 155500	16 Oct 2015	18.5	8–9	4 (3+1)	16.2 ± 0.5 (8.0–22.0)	102	<0.0001
1821	III	LPN Snežnik (331)	M1B3	491500 143500	23 Dec 2015	15.0	8–9	4 (2+2)	16.3 ± 0.4 (12.0–20.5)	54	<0.0001

[a] Identity number of the doe in the sample set

[b] Hunting management district

[c] Culling location in 1 × 1 km grid

[d] Coordinates of centroids of every single quadrant

[e] Body mass less viscera but with head and feet on

[f] Number of CL (L: in left ovary; R: in right ovary), reflecting potential litter size

[g] For comparison with each exceptional breeder data on all adult does harvested in the relevant hunting management district in the relevant year and month are presented (e.g. for the doe with ID-79 for all does, shot in the District II in September 2013). Statistical comparison was made by two-sided *t* test for differences (StatSoft 2014)

Table 2 Data on roe deer females with potential litter size >3, harvested in Arezzo Province (Tuscany, Central Italy) in the period 1 January–15 March, accompanied by data on mean body mass of all adult females, harvested in the same year/month and in the same hunting management district (source: Provincial Administration of Arezzo–official data)

ID of doe	District	Hunting ground	Coordinates[a] (UTM-WGS84)	Date of cull	Body mass (kg)	Age (years)	CL (*N*) (L+R)	Foetuses[b]		Mean body mass (kg) of does in the district		
								N (L+R)	Sex (length (cm); weight (g))	Mean ± 1.96*SE (min–max)	N	*P* value
45188	I	2062	726206 4839208	7 Mar 2011	17.0	3–4	4 (2+2)	5 (3+2)	1L♀ (12.9; 61.1) 2L♀ (12.2; 56.0) 3L♂ (12.3; 58.1) 1R♀ (12.3; 53.4) 2R♀ (12.2; 60.4)	17.7 ± 0.6 (14.5–22.2)	32	0.05
45428	I	3013	724658 4828976	14 Mar 2011	19.8	5–7	3 (1+2)	4 (2+2)	1L♀ (17.5; 172.1) 2L♂ (18.0; 198.4) 1R♀ (18.5; 198.1) 2R♀ (17.5; 185.2)	17.7 ± 0.6 (14.5–22.2)	32	<0.01
51352	II	24006	722289 4797469	5 Mar 2014	19.6	2	4 (2+2)	4 (2+2)	1L♂ (16.5; 180.1) 2L♂ (17.3; 175.2) 1R♀ (16.0; 163.2) 2R♀ (15.8; 170.1)	18.0 ± 0.4 (12.0–22.1)	92	<0.01
54119	I	14011	737803 4849793	17 Feb 2014	16.8	5–7	4 (3+1)	3 (2+1)	1L♂ (7.6; 17.5) 1R♀ (7.0; 13.9) 2R♂ (7.0; 16.1)	17.8 ± 0.4 (11.0–23.0)	85	<0.01
56077	II	8041	723049 4812173	23 Jan 2014	17.2	3–4	4 (2+2)	4 (2+2)	1L♂ (9.1; 30.3) 2L♂ (9.0; 29.3) 1R♂ (9.1; 31.4) 2R♂ (9.3; 30.7)	18.1 ± 0.6 (10.8–23.3)	58	<0.05
57395	III	17001	699391 4820239	20 Feb 2014	21.8	3–4	4 (3+1)	5 (3+2)	1L♀ (8.0; 15.8) 2L♂ (8.1; 16.7) 3L♂ (8.2; 16.6) 1R♂ (7.5; 15.2) 2R♂ (7.3; 13.8)	18.8 ± 0.4 (13.0–25.0)	92	<0.01
57396	III	17001	699391 4820239	20 Feb 2014	16.9	3–4	4 (2+2)	4 (2+2)	1L♀ (10.0; 30.2) 2L♂ (10.1; 31.0) 1R♂ (10.1; 30.2) 2R♂ (11.2; 41.3)	18.8 ± 0.4 (13.0–25.0)	92	<0.05

[a] Coordinates of centroids of every single hunting ground

[b] Number of foetuses in the left (L) or right (R) horn of the uteri with basic data. For others, see notes below Table 1

which all potential litters >3 offspring were found both in Slovenia and Italy (Tables 1 and 2). In healthy adult roe deer, losses due to resorption of foetuses are minimal, generally in the order of 1–4%, though they may be as high as 9–22% among sick individuals (Danilkin 1996). In our population, losses due to resorption of foetuses are indeed very low, i.e. <1% (37 cases out of 5023 foetuses in the Italian subset), indicating that the number of offspring would not substantially differ from the litter size in uteri.

Although we are not able to predict surely that any of does with exceptional (potential) litter size would actually give birth to four or even five fawns, very low resorption of foetuses together with low implantation failure found also in our sample sets (Slovenia: 5.9%, 64 F and 68 CL; Italy: 8.6%, 4896 F and 5356 CL) indicate that at least some of them would. Moreover, it is worth to note that the two does with five foetuses had only 4 CL (Table 2), suggesting a very rare case of monozygotic twins in roe deer. Based on this finding, the actual litter size predicted on the basis of CL counts can in some cases even be underestimated and not only overestimated. Considering the risk for the resorption of foetuses, it is also important that in both cases all five foetuses were of comparable size (Table 2), indicating that none of them had predominant exposure to resorption/abortion. In the first case (doe ID-45188), the difference in weight between the largest and the smallest foetuses was 14.8%, and in the second case (ID-57395) this difference was 17.3%. Very interesting is also comparison of the length/weight of foetuses in exceptionally large litters with the average size of foetuses in does, shot in the same HMD in 14-day interval around the harvesting date of the exceptional breeders (Table S2): both mean length and weight of litters composed by five foetuses were significantly smaller in comparison with litters composed by singletons or twins (but in one case (ID-45188) they tend to be larger in comparison with the only pack of triplets); however, in two out of four cases of quadruplets they were significantly larger in comparison with triplets and even twins, and in other two cases they were of comparable sizes with all litters (even with singletons), indicating their performance would not be inferior to normal litters (see also Fig. S2).

In general, roe deer females with higher body mass produce larger litters (e.g. Andersen and Linnell 2000; Hewison and Gaillard 2001; Focardi et al. 2002; Macdonald and Johnson 2008). Similarly, within the studied population in Slovenia proportion of females carrying more than one (and two) CL markedly increased with the body mass both in yearlings and adult does, and as much as 11% of adults with body mass >18.0 kg had three or more CL (Flajšman et al. 2017). However, while the probability to produce litters >2 offspring clearly increased with the body mass (ibid.), does with four or five CL (Slovenian dataset) and with four or five foetuses (Italian dataset) were not in all cases heavier in comparison with averaged does, harvested in the same HMD and in the same period (Tables 1 and 2). Indeed, while 6 (ID-487, ID-540, ID-1538 for Slovenian dataset, and ID-57395, ID-45428, ID-51352 for Italian dataset) out of 13 does with exceptionally large potential litters had significantly higher body mass in comparison with the mean body mass of all relevant does, 5 of them (ID-79, ID-1821 for Slovenian dataset, and ID-45188, ID-56077, ID-57396 for Italian dataset) were even significantly lighter. Particularly interesting is that the doe with five CL, shot in Slovenia in September 2013, had a body mass of only 13.0 kg, indicating that this exceptional ovulation might be a stochastic episode rather than a reproductive performance of a very vital individual. However, it is also interesting that when analysing more advanced stage of pregnancy (data from Italian dataset), the greatest allocation in offspring production was in two does (with five foetuses) with body mass similar to the medium value recorded in its HMD (ID-45188) or with significantly higher body mass (ID-57396). Because environmental conditions during the reproduction are unpredictable, it may be advantageous for mammalian females to conceive, especially because ovulation is not energetically demanding, while later facing the possibility of losing offspring following unfavourable stochastic events (Cresswell et al. 1992; Hewison and Gaillard 2001; Simard et al. 2014; Frauendorf et al. 2016). Thus, females should adjust their reproductive effort prior to substantial investment. For roe deer, due to delayed implantation, this adjustment may occur at ovulation/fertilization during the summer rut or at implantation in mid-winter (Hewison and Gaillard 2001). Indeed, for income breeders where females rely on food intake rather than on fat reserves for reproduction, Hewison and Gaillard (2001) suggested that a two-step process shapes patterns of reproductive output: body mass first sets an upper limit to potential litter size at conception, than reproductive output is limited mainly by senescence and climatic severity through implantation failure. However, while these processes shape the reproductive performance of roe deer females in general, i.e. by influencing fertility and average litter sizes within and among populations (which are both predominantly determined by body mass and its age-related influence; see Flajšman et al. 2017), some does can have exceptionally large litters—up to 5 offspring—even when their phenotypic quality is not remarkably high.

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Compliance with ethical standards

Conflicts of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All roe deer females used in the research were harvested during the regular hunting activity, i.e. prescribed by the national authorities of Slovenia and Italy within the yearly hunting management plans. Therefore, no animal was shot or killed by any other means for the purposes of the research in which we used reproductive organs of already dead animals.

Informed consent Informed consent was obtained from all individual participants included in the study.

Data availability statement The datasets during and/or analysed during the current study are available from the corresponding author on reasonable request.

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