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Effects of population density and female body mass on litter size in European roe deer at a continental scale

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Abstract

Roe deer (*Capreolus capreolus*) has a wide distributional range in Europe and inhabits a broad range of habitats and environmental conditions. Thus, populations of roe deer show substantial variation in demographic parameters. We aimed to determine whether body mass and population density—which influence the reproductive potential of roe deer at a local scale—affect their reproductive potential at a biogeographical scale as well. We reviewed the literature (covering years 1948–2015) on in utero litter size in roe deer from 59 locations in 14 countries in Europe. Across study sites, mean litter size varied from 1.0 to 2.4 embryo or corpora lutea per female, and population density ranged from 4.5 to 73.5 individuals/km^2. Mean body mass varied from 11.2 to 20.8 kg in subadult females and from 12.1 to 22.4 kg in adult females. Between 46° and 56° N, body mass of females did not show a significant trend of increase, whereas between 56° and 63° N, it increased with latitude (Bergmann's rule). We used linear mixed-effects models (LMMs) to analyse the influence of body mass and population density (analysed separately) on litter size. Females with larger body mass produced larger litters, and this pattern was pronounced at both higher and lower latitudes. Higher population densities negatively affected litter size in a sample of all females. This macroecological analysis showed that factors influencing the reproductive potential of roe deer females at local scales produce similar effects at the biogeographical scale.

Keywords *Capreolus capreolus* · In utero litter size · Density-dependence · Subadult and adult females · Latitude · Bergmann's rule · Europe

Introduction

Roe deer (*Capreolus capreolus*) is the most abundant European ungulate with a distributional range spanning from the south of Spain to northern Norway and from the British

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Isles to the Caucasus (Andersen et al. 1998; Apollonio et al. 2010). Roe deer occupy a wide variety of natural and human-altered habitats (Andersen et al. 1998) and face diverse environmental and climatic conditions, which influence their reproduction—the major component of population dynamics (Andersen and Linnell 2000). The most important parameter of reproductive potential in roe deer females is litter size. Studies on local populations have shown that the number of offspring in a litter varies with individual female quality (body size and body mass; Kjellander et al. 2004; Hamel et al. 2009; Flajšman et al. 2017a), population density and demographic structure (Andersen and Linnell 2000, Nilsen et al. 2009), weather conditions, landscape structure, habitat quality (Nilsen et al. 2004; Toïgo et al. 2006), and the genetic characteristics of individual females within populations (Hewison 1997).

Body mass has been reported to be a strong determinant of female fertility (probability of pregnancy) in red deer (*Cervus elaphus*), moose (*Alces alces*), caribou (*Rangifer tarandus*), white-tailed deer (*Odocoileus virginianus*), and roe deer (Saether and Haagerund 1985; Gaillard et al. 1992;

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Pachkowski et al. 2013; Simard et al. 2014; Borowik et al. 2016). In roe deer, litter size varies from 1 to 5 (Danilkin 1996; Flajšman et al. 2017b). Heavier females have larger litters and produce more offspring (Danilkin 1996; Andersen and Linnell 2000; Hewison and Gaillard 2001; Focardi et al. 2002; Macdonald and Johnson 2008; Flajšman et al. 2014, 2017a), though becoming pregnant and then carrying more than one embryo generally require the reaching of a threshold body mass (Focardi et al. 2002; Flajšman et al. 2014). Furthermore, body mass of ungulates often varies latitudinally (Bergmann's rule; Langvatn and Albon 1986; Sand et al. 1995), so this needs to be taken into account in any meta-analysis at biogeographical scale.

In ungulates, higher population densities can indirectly affect reproduction through social stress and lower per capita availability of food (Hewison 1996; Body et al. 2011; Couturier et al. 2012). This causes a decrease in the number of pregnant females in the population, leads to smaller litters, and postpones the age of the first breeding (Focardi et al. 2002; Bonenfant et al. 2009). The negative effect of high population density on the reproductive rates of ungulates has been reported both in a temporal context in one population (long-term demographic data; e.g. Mysterud et al. 2007) and in a spatial context through the comparison of different populations (Andersen et al. 1998; Andersen and Linnell 2000; Focardi et al. 2002). The inverse relationship between population density and fertility is due to the deterioration of female body condition caused by intraspecific competition for food resources (Stewart et al. 2005; Tavecchia et al. 2005).

To date, studies on roe deer reproduction have been performed in single local populations or have compared a relatively small number of contrasting populations (Hewison and Gaillard 2001; Gaillard et al. 2003; Macdonald and Johnson 2008). In this paper, we aimed to review locally obtained findings from the species' European range. Drawing on a survey of the scientific literature from 14 European countries, we collated data on roe deer population density, mean body mass of females, and in utero litter size. Based on the findings from local studies, we expected that: (1) litter size would be positively related to female body mass, (2) higher population densities would negatively affect litter size, and (3) these effects would be stronger in subadult than in adult females. The latter prediction is based on studies on large ungulates that showed that fertility of subadult primiparous females is more affected by body mass than that of adult females (Gaillard et al. 2000; Borowik et al. 2016).

Material and methods

We collected published data on roe deer in utero litter size by searching scientific databases (namely ISI Web of Science, Scopus, and ResearchGate), using the following keywords:

roe deer, *Capreolus capreolus*, reproduction, reproductive parameters, litter size, and corpora lutea. Apart from one set of data from Slovenia (Flajšman et al. 2015), we used only peer-reviewed papers on free-ranging populations. For our analyses, we searched for the number of corpora lutea or number of embryos per reproducing female in all females (when age was not defined), and subadult (12–24 months old) and adult females (> 24 months old). The age classes were determined by examination of the tooth eruption pattern (Aitken 1975). Based on previous findings (Borg 1970; Strandgaard 1972; Flajšman et al. 2017b), we assumed that the embryonic loss in the first period of gestation was negligible. Therefore, the data on the number of corpora lutea and embryos were analysed together. In total, 27 studies reporting on 59 local populations in 14 European countries were included in the analysis (Fig. 1, Table S1 in Supplementary material).

For each of the studied sites (when available), we gathered information on population density (all age and sex classes combined; number of individuals/km^2) and mean body mass of females in a population (kg). Roe deer population densities were estimated by a diverse array of methods (Table S1, Supplementary material), including drive-counts, capture-mark recapture, vantage-point observations, pellet-group counts, and recalculation from harvest data controlled by pellet-group counts. Three sources did not provide information on the counting method. Although the use of diverse methods inevitably created additional variation in the dataset, we do not believe this caused any systematic error that could have led to a false litter size—population density relationship. Also, the range of the reported density variation (the minimum and maximum values differed by an order of magnitude) was far beyond the possible errors of the counting methods.

The majority of the studies reported dressed or eviscerated body mass. In cases where body mass of live animals was reported, we multiplied live body mass by 0.75 to obtain the eviscerated body mass (after Krže 2000). Google Maps (http://maps.google.co.uk) was used to determine the coordinates of the approximate midpoints of the study sites. We tested for differences in body mass and litter size between subadult and adult females with a Mann-Whitney-Wilcoxon test.

We used linear mixed-effects models (LMMs,"lme4" package; Bates and Sarkar 2006) to separately analyse the effects of body mass and population density on the litter size of roe deer females. In the analyses, we included only those populations where data on either density (all females—30 populations, subadults—19, and adults—27) or body mass of females (all females—38 populations, subadults—29, and adults—30) were available (Fig. 1). Only a few populations had information on both body mass and population density (all females—13 populations, subadults—11, adults—11), hence the sample size was too small to analyse the combined effect of these factors on roe deer litter size.

Fig. 1 Locations of studies on roe deer (*Capreolus capreolus*) litter size in Europe, conducted in 1948–2015. Black points are data used in the linear mixed-effects models (LMMs). Open points are data on litter size only used for calculating the mean values (in Table 1). The list of data and sources is given in Table S1 (Supplementary material)
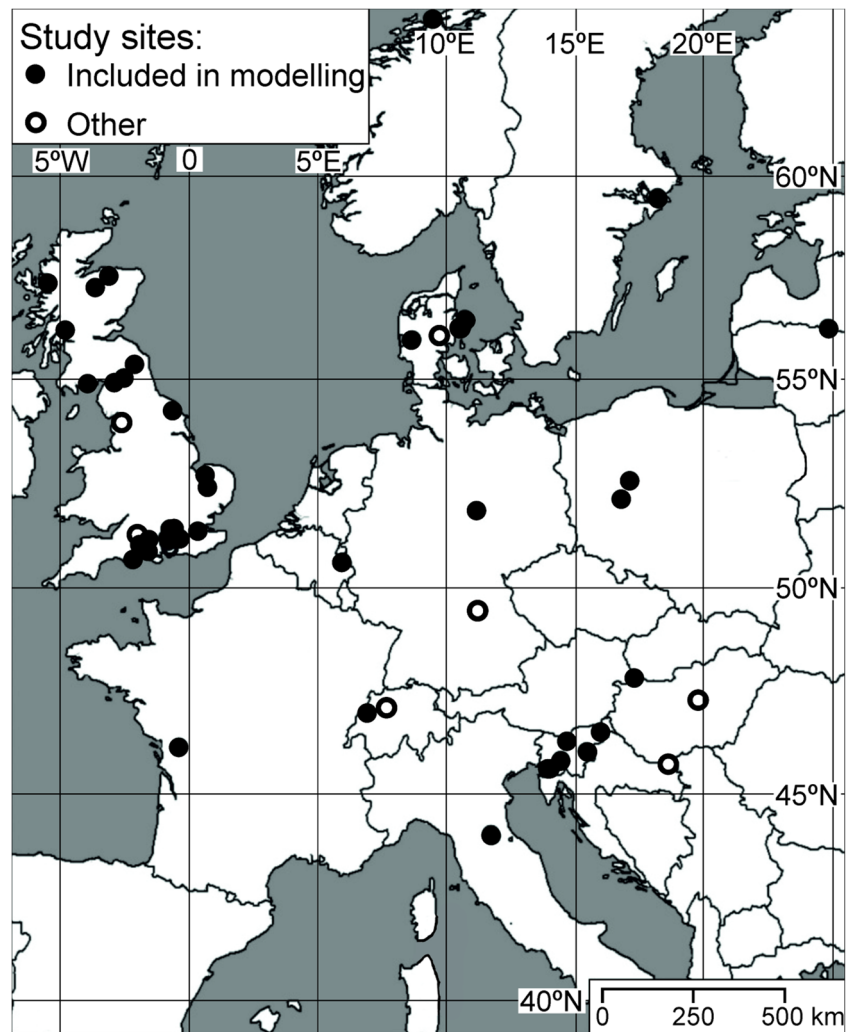
For some populations, we had a data series from different years; thus, we assigned population identification (ID) as a random factor in the mixed modelling framework (Zuur et al. 2009). Finally, we ran six models, which—for all females, subadults, and adults—tested the effects of body mass or population density on litter size. We checked the normality and homoscedasticity in the distribution of the models' residuals by inspecting their diagnostic plots. In the model testing the effect of body mass on litter size in all females, the diagnostic plot indicated the presence of an influential outlier, which was removed from further analyses. Applied variograms did not show significant spatial autocorrelation in model residuals.

In addition, we tested if female body mass increased with latitude by fitting a segmented regression ("segmented" package; Muggeo 2016) to each of the analysed datasets. For each subset, segmented regression indicated the breakpoint latitudes, the significance of which was tested with Dories' test for a change of slope. We found that above 56° N female body mass increased northwards, in which case the positive effect

of body mass on litter size could have been explained by Bergmann's rule. We verified this hypothesis by dividing each set of body mass data (all females, subadults, and adults) into southern and northern subsets and tested the effect of body mass on litter size for the two latitudinal subsets separately. All statistical analyses were conducted in R version 3.3.2 (R Development Core Team 2016).

Results

Across study sites, roe deer population density ranged from 4.5 to 73.5 individuals/km^2 (Table 1). There was on average 1.79 ($\pm$ 0.03 SE) embryo or corpora lutea per pregnant female, and the mean litter size was significantly lower in subadult (1.63 $\pm$ 0.05) than in adult females (1.90 $\pm$ 0.04) (Mann-Whitney-Wilcoxon test, $W = 1293$, $P < 0.001$). Higher population densities negatively affected litter size; in a sample of all females, mean litter size declined from 2.0 to 1.4 ($P = 0.004$;

Table 1 Population density, female body mass, and litter size in roe deer populations studied in 1948–2015 throughout Europe. Distribution of the study sites is shown in Fig. 1, and the list of data and sources in Table S1 (Supplementary material). *Litter size*, number of embryos or *corpora lutea* per pregnant female; *N*, number of populations; *All females*, roe deer populations where no information on female age was available

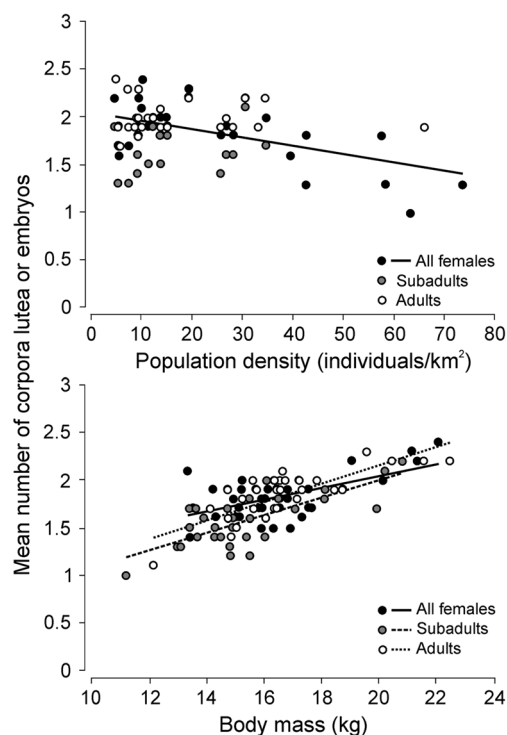| Parameter	Mean ± SE	Min–max	*N*
Population density (inds/km^2)	24.5 ± 3.5	4.5–73.5	33
Body mass (kg)			
All females	16.5 ± 0.3	11.7–22.1	60
Subadults	15.4 ± 0.4	11.2–20.8	30
Adults	17.0 ± 0.4	12.1–22.4	31
Litter size			
All females	1.79 ± 0.03	1.0–2.4	71
Subadults	1.63 ± 0.05	1.0–2.2	36
Adults	1.90 ± 0.04	1.1–2.4	47

Fig. 2 Upper panel: Influence of population density (both sexes and all age classes combined) on litter size of roe deer females in Europe. Full results of the linear mixed-effects models (LMMs) and estimates of model parameters are given in Table 2. Trend line is drawn for the significant effect only. Lower panel: Influence of mean body mass of females on litter size of roe deer in Europe. Full results of linear mixed-effects models (LMMs) and estimates of model parameters are given in Table 3

Table 2, Fig. 2). Population density did not affect mean litter size of subadult and adult females (Table 2).

The mean (± SE) body mass was 16.5 (± 0.3) kg and was significantly lower in subadult (15.4 ± 0.4 kg) than in adult females (17.0 ± 0.4 kg) (Mann-Whitney-Wilcoxon test, $W =$ 732, $P = 0.001$; Table 1). The change in the body mass−latitude relationship at the breakpoints of 56°47′ to 57°49′N (see below) was highly significant (Dories' test for a change of slope, P from 0.001 to 0.008). Between 46° and 56° N, body mass of female roe deer did not show a significant trend of increase contrary to our prediction (P from 0.41 to 0.55), whereas between 56° and 63°N, it increased with latitude,

and this pattern appeared in subadult, adult, and all females which supported our prediction (R^2 from 0.75 to 0.83; P from 0.01 to 0.05; Fig. 3).

Table 2 The effect of population density on litter size of roe deer throughout Europe. Results of linear mixed-effects models (LMMs). R^2, likelihood-ratio based on pseudo-*R*-squared; *N*, number of populations; *All females*, roe deer populations where no information on female age was available

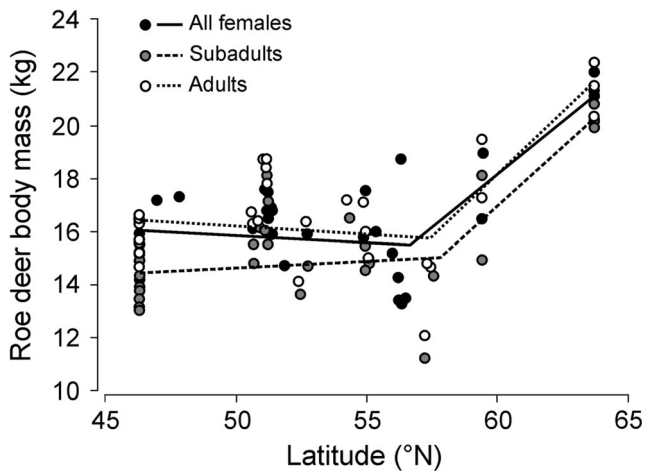| Variables	Fixed effects			Random effect	R^2	*N*
	Estimate ± SE	*t* value	*P* value	SD		
All females					0.65	30
Intercept	2.03 ± 0.08	26.69	< 0.001			
Density	− 0.008 ± 0.002	− 3.35	0.004			
Population ID				0.18		
Subadults					0.07	19
Intercept	1.64 ± 0.12	13.54	< 0.001			
Density	0.0004 ± 0.007	0.06	0.95			
Population ID				0.15		
Adults					0.004	27
Intercept	2.02 ± 0.06	34.50	< 0.001			
Density	− 0.001 ± 0.003	− 0.32	0.76			
Population ID				<0.001		

Fig. 3 Latitude-related changes in the eviscerated body mass of females in roe deer populations. Body mass breakpoints were estimated using segmented regression. All females, $R^2 = 0.52$, $P < 0.001$; subadults, $R^2 = 0.49$, $P = 0.29$; adults, $R^2 = 0.45$, $P = 0.14$. Body mass increase with latitude is only significant for northern regions (56°–63°N; P for slopes from 0.01 to 0.05)

Female body mass had a significant and strong positive effect on litter size both in subadult ($P = 0.001$) and adult females ($P = 0.001$) as well as in the sample of all females ($P = 0.004$; Table 3). An increase body mass (subadults: from 11.2 to 20.8 kg; adults: from 12.1 to 22.4 kg) resulted in an increase in litter size by 0.88 for subadults, and 1.0 for adults (Fig. 2). In other words, in female roe deer, near doubling of body mass increased the number of embryos by almost 1.

As female body mass varied latitudinally (see Fig. 3), we analysed the litter size—body mass relationship separately for two subsamples of data (as indicated by the results of the segmented regression): (1) all females—populations located below and above 56°49′ N, (2) subadult females—below and above 57°49′ N, and (3) adult females—below and above

57°26′ N. The pattern of heavier females producing larger litters appeared at both higher and lower latitudes, as predicted. However, due to small sample sizes, this relationship was only significant for subadult and adult females in the southern populations ($P = 0.04$, $R^2 = 0.35$ and $P = 0.02$, $R^2 = 0.48$, respectively), whereas this relationship was only significant for all females in the northern populations ($P = 0.01$, $R^2 = 0.75$; Fig. 4). To sum up, roe deer populations with high body mass were more likely to have larger litters even when taking into account Bergmann's rule.

Discussion

Our meta-analysis of factors shaping roe deer litter size at a continental scale is—to our best knowledge—the first such macro-ecological study of this species. Compared to investigations of local roe deer populations, our study operated on values averaged for populations (and not on variation among individuals), so it ignored intra-population variation in reproductive parameters. On the other hand, in such a large-scale study, the variation in both extrinsic and intrinsic factors affecting reproduction is substantially larger than could be expected in any local population, which gives the opportunity to cover a broad spectrum of a species' response to that variation.

Generally, we showed that individual and population variables that influence the reproductive potential of roe deer females in local populations had a similar effect at a much broader biogeographical scale: litter size declined with growing population density, and it increased with higher body mass of females. Moreover, the body mass–litter size relationship observed at the biogeographical scale was not the sole effect of Bergmann's rule, as it also held true at lower latitudes, where female body mass was not correlated to latitude. At

Table 3 The effect of female body mass on litter size in roe deer populations throughout Europe. Results of linear mixed-effects models (LMMs). R^2, likelihood-ratio based on pseudo-R-squared; N, number of populations; *All females*, roe deer populations where no information on female age was available

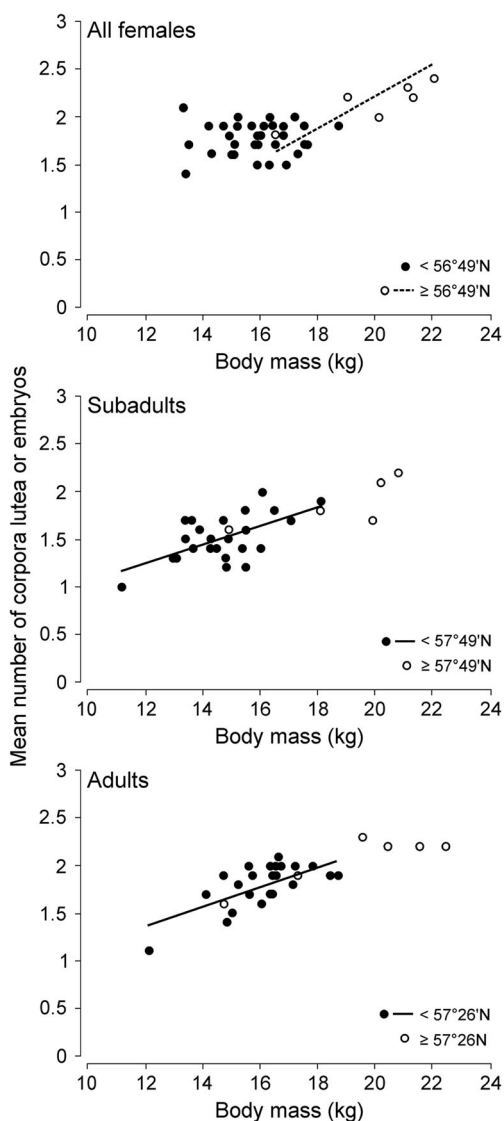| Variables	Fixed effects			Random effect	R^2	N
	Estimate ± SE	t value	P value	SD		
All females					0.35	38
Intercept	0.81 ± 0.26	3.15	0.004			
Body mass	0.06 ± 0.01	3.90	0.004			
Population ID				0.06		
Subadults					0.54	29
Intercept	0.17 ± 0.25	0.66	0.52			
Body mass	0.09 ± 0.02	5.64	0.001			
Population ID				<0.001		
Adults					0.62	30
Intercept	0.22 ± 0.27	0.83	0.41			
Body mass	0.10 ± 0.02	6.05	0.001			
Population ID				0.11		

Fig. 4 Influence of female body mass on litter size of roe deer in European populations located below and above: (1) 56°49′ N for all females, (2) 57°49′ N for subadults, and (3) 57°26′ N for adult females. Trend lines are drawn for significant effects. Breakpoints for the divisions into two latitudinal subsets of populations were shown by the results of the segmented regressions (see Fig. 3)

Scottish Blackface sheep breed (Gunn and Doney 1975), and wild boar (*Sus scrofa*) (Servanty et al. 2009; Jelenko et al. 2014). Heavier females of roe deer had larger litters and produced more offspring than lighter ones (Andersen and Linnell 2000; Focardi et al. 2002; Flajšman et al. 2014, 2017a; this study).

Melis et al. (2009) found that—in the absence of large carnivores—food availability was the major factor shaping population density of roe deer in Europe and proposed that this was caused by competition for food driving density-dependence in population growth rates. Density-dependent effects in the life-history traits of large mammals most often occur at high densities, when populations approach carrying capacity (Fowler 1981; Gaillard et al. 2000). This is in line with the long-term (over 100 years) data series from eastern Poland showing clear density-dependence in the roe deer population (Jędrzejewska et al. 1997). In general, an increase in population density leads to unequal partitioning of food resources among individuals (as a result of contest competition; Łomnicki 1978) and a reduction in reproductive output (from ovulation to weaning) and increase in mortality (reviewed in: Bonenfant et al. 2009). Indeed, our meta-analysis of population data at the biogeographic scale clearly showed that litter size decreased with an increase in roe deer density.

Although we analysed the effects of body size and population density on litter size separately, both variables emerged as significant driving mechanisms in roe deer populations, similarly to other species of ungulates (e.g. moose: Gingras et al. 2014; Soay sheep *Ovis aries*: Forchhammer et al. 2001; saiga antelope *Saiga tatarica*: Coulson et al. 2000). Yet, in our models the two predictor variables explained 54–56% of the variation in litter size. Therefore, although body mass and population density may drive litter size of roe deer at a biogeographical scale, other factors such as variation in local climatic conditions and vegetation productivity, life-history traits, predation pressure, different hunting, and management regimes as well as evolutionary differences in life history traits and adaptations among various phylogenetic lineages of the species may confound the explanatory power of these predictors. Pan-European study on variation in roe deer population density (Melis et al. 2009) showed that the presence of large predators especially the Eurasian lynx (*Lynx lynx*) is the crucial factor shaping roe deer population response to food resources (approximated by habitat productivity and forest cover), whereas different hunting regimes did not significantly affect the observed variation in densities. Recent studies have shown that in the eastern part of its range (east of central Poland and Hungary), roe deer populations carry a large proportion of mtDNA haplotypes of the 'Siberian' lineage—the result of past hybridization with Siberian roe deer (*C. pygargus*) (Lorenzini et al. 2014; Matosiuk et al. 2014; Olano-Marin et al. 2014). It remains unknown whether the 'Siberian' lineage differs from the 'native' lineages of

the continental scale, mean litter size of subadult females was 15% smaller than that of adult females. An age-related difference in roe deer litter size was discernible across the whole range of population density and body mass variation.

The main pathway by which density-dependence affects reproduction is via the body mass of females. Individuals in good condition attain the threshold size, reproduce earlier, and have higher fecundity than females in poor condition (Bonenfant et al. 2009). This pattern has been observed in many species of ungulates, including red deer (Albon et al. 1983; Borowik et al. 2016), reindeer (Gerhart et al. 1997), Alaskan caribou (*R. tarandus granti*) (Adams and Dale 1998), moose (Testa and Adams 1998; Garel et al. 2009),

European roe deer in life history traits and reproductive biology. Due to the availability of published material, the dataset used in this paper mostly comprised local populations free of lynx and wolf (*Canis lupus*) predation (comp. Jędrzejewski et al. 2011) and located beyond the western limits of the 'Siberian' lineage. Thus, the potential bias resulting from these two factors was negligible in our dataset. However, it should be kept in mind that the patterns revealed in our meta-analysis may only hold true in the areas of Europe covered by the studied data points, in populations not subject to predation and in 'pure' lineages of European roe deer.

References

Adams LG, Dale BW (1998) Reproductive performance of female Alaskan caribou. J Wildl Manag 62(4):1184–1195. https://doi.org/10.2307/3801982

Aitken RJ (1975) Cementum layers and tooth wear as criteria for ageing roe deer. J Zool 175:15–28

Albon SD, Mitchell B, Staines BW (1983) Fertility and body weight in female red deer: a density-dependent relationship. J Anim Ecol 52(3):969–980. https://doi.org/10.2307/4467

Andersen R, Linnell JDC (2000) Irruptive potential in roe deer: density-dependent effects on body mass and fertility. J Wildl Manag 64(3):698–706. https://doi.org/10.2307/3802739

Andersen R, Duncan P, Linnell JDC (1998) The European roe deer: the biology of success. Scandinavian University Press, Oslo

Apollonio M, Andersen R, Putman R (2010) European ungulates and their management in the 21st century. Cambridge University Press, Cambridge

Bates D, Sarkar D (2006) lme4: linear mixed-effects models using S4 classes. R package version .99875–.8

Body G, Ferté H, Gaillard JM, Delorme D, Klein F, Gilot-Fromont E (2011) Population density and phenotypic attributes influence the level of nematode parasitism in roe deer. Oecologia 167(3):635–646. https://doi.org/10.1007/s00442-011-2018-9

Bonenfant C, Gaillard JM, Coulson T, Festa-Blanchet M, Loison A, Garel M, Loe LE, Blanchard P, Petorelli N, Owen-Smith N, du Toit J, Duncan P (2009) Empirical evidence of density-dependence in populations of large herbivores. Advan Ecol Res 41:313–357. https://doi.org/10.1016/S0065-2504(09)00405-X

Borg K (1970) On mortality and reproduction of roe deer in Sweden during the period 1948-1969. Swedish Sportmen's Association 7: 121–149

Borowik T, Wawrzyniak P, Jędrzejewska B (2016) Red deer (*Cervus elaphus*) female fertility and early survival of young in a low density population subject to predation and hunting in Central Europe. J Mammal 97(6):1671–1681. https://doi.org/10.1093/jmammal/gyw133

Coulson T, Milner-Gulland EJ, Clutton-Brock TH (2000) The relative roles of density and climatic variation on population dynamics and fecundity rates in three contrasting ungulate species. P Roy Soc of Lond B Bio 267(1454):1771–1779. https://doi.org/10.1098/rspb.2000.1209

Couturier S, Otto RD, Cote SD, Glenn L, Mahoney SP (2012) Body size variations in caribou ecotypes and relationships with demography. J Wildl Manag 74:395–404

Danilkin A (1996) Behavioural ecology of Siberian and European roe deer. Chapman & Hall, wildlife ecology and behaviour series. Springer, Amsterdam

Flajšman K, Jelenko I, Pokorny B (2014) Reproductive potential of roe deer in Slovenia. Balkan J Wildl Res 1:20–25

Flajšman K, Jelenko-Turinek I, Pokorny B (2015) Razmnoževalni potencial in genetske značilnosti srnjadi (*Capreolus capreolus* L.) v Sloveniji (project report). Institute ERICo Velenje and Slovanian Forestry Institute, Velenje and Ljubljana (In Slovenian)

Flajšman K, Jerina K, Pokorny B (2017a) Age-related effects of body mass on fertility and litter size in roe deer. PLoS One 12(4): e0175579. https://doi.org/10.1371/journal.pone.0175579

Flajšman K, Pokorny B, Chirchella R, Bottero E, Mattioli L, Apollonio M (2017b) I can produce more offspring as you can imagine: first records on exceptionally large litters in central/southern Europe. Eur J Wildl Res 63(3):42. https://doi.org/10.1007/s10344-017-1102-9

Focardi S, Pellicioni ER, Petrucco R, Toso S (2002) Spatial patterns and density dependence in the dynamics of a roe deer (*Capreolus capreolus*) population in central Italy. Oecologia 130(3):411–419. https://doi.org/10.1007/s00442-001-0825-0

Forchhammer MC, Clutton-Brock TH, Lindstrom J, Albon SD (2001) Climate and population density induce long-term cohort variation in a northern ungulate. J Anim Ecol 70(5):721–729. https://doi.org/10.1046/j.0021-8790.2001.00532.x

Fowler CW (1981) Density dependence as related to life history strategy. Ecology 62(3):602–610. https://doi.org/10.2307/1937727

Gaillard J-M, Sempere AJ, Boutin JM, Van Laere G, Boisaubert B (1992) Effects of age and body weight on the proportion of females breeding in a population of roe deer (*Capreolus capreolus*). Can J Zool 70(8):1541–1545. https://doi.org/10.1139/z92-212

Gaillard J-M, Festa-Bianchet M, Yoccoz NG, Loison A, Toïgo C (2000) Temporal variation in fitness components and population dynamics of large herbivores. Annu Rev Ecol Syst 31(1):367–393. https://doi.org/10.1146/annurev.ecolsys.31.1.367

Gaillard J-M, Duncan P, Delorme D, Van Laere G, Pettorelli N, Maillard D, Renaud G (2003) Effects of hurricane Lothar on the population dynamics of European roe deer. J Wildl Manag 67(4):767–773. https://doi.org/10.2307/3802684

Garel M, Solberg EJ, Saether BE, Grøtan V, Tufto J, Heim M (2009) Age, size, and spatiotemporal variation in ovulation patterns of a seasonal breeder, the Norwegian moose (*Alces alces*). Am Nat 173(1):89–104. https://doi.org/10.1086/593359

Gerhart KL, Ruussell DE, Van de Wetering D, White RG, Cameron RD (1997) Pregnancy of adult caribou (*Rangifer tarandus*): evidence for lactational infertility. J Zool 242(1):17–30. https://doi.org/10.1111/j.1469-7998.1997.tb02926.x

Gingras J, Couturier S, Côté SD, Tremblay J-P (2014) Opposite responses of body condition and fertility in adjacent moose populations. J Wild Manage 78(5):830–839. https://doi.org/10.1002/jwmg.729

Gunn RG, Doney JM (1975) The interaction of nutrition and body condition at mating on ovulation rate and early embryo mortality in

Scottish blackface ewes. J AgricSci 85(03):465–470. https://doi.org/10.1017/S0021859600062341

Hamel S, Gaillard JM, Festa-Bianchet M, Côté SD (2009) Individual quality, early-life conditions, and reproductive success in contrasted populations of large herbivores. Ecology 90(7):1981–1995. https://doi.org/10.1890/08-0596.1

Hewison AJM (1996) Variation in the fecundity of roe deer in Britain: effects of age and body weight. Acta Theriol 41:187–198. https://doi.org/10.4098/AT.arch.96-18

Hewison AJM (1997) Evidence for a genetic component of female fecundity in British roe deer from studies of cranial morphometrics. Funct Ecol 11(4):508–517. https://doi.org/10.1046/j.1365-2435.1997.00120.x

Hewison AJM, Gaillard JM (2001) Phenotypic quality and senescence affect different components of reproductive output in roe deer. J Anim Ecol 70(4):600–608. https://doi.org/10.1046/j.1365-2656.2001.00528.x

Jędrzejewska B, Jędrzejewski W, Bunevich AN, Miłkowski L, Krasiński ZA (1997) Factors shaping population densities and increase rates of ungulates in Białowieża Primeval Forest (Poland and Belarus) in the 19th and 20th centuries. Acta Theriol 42:399–451. https://doi.org/10.4098/AT.arch.97-39

Jędrzejewski W, Apollonio M, Jędrzejewska B, Kojola I (2011) Ungulate—large carnivore relationships in Europe. In: Putman R, Apollonio M, Andersen R (eds) Ungulate management in Europe: problems and practices. Cambridge University Press, Cambridge, pp 284–318. https://doi.org/10.1017/CBO9780511974137.011

Jelenko I, Marolt J, Flajšman K, Stergar M, Jerina K, Pokorny B (2014) Oplojenost samic divjih prašičev v Sloveniji v letu 2012/13. Lovec 97:556–561

Kjellander P, Hewison AJM, Liberg O, Angibault J-M, Bideau E, Cargnelutti B (2004) Experimental evidence for density-dependence of home-range size in roe deer (Capreolus capreolus L.): a comparison of two long-term studies. Oecologia 139(3):478–485. https://doi.org/10.1007/s00442-004-1529-z

Krže B (2000) Srnjad: biologija, gojitev, ekologija. Zlatorogova knjižica. Lovska zveza Slovenije, Ljubljana (In Slovenian)

Langvatn R, Albon SD (1986) Geographic clines in body weight of Norwegian red deer: a novel explanation of Bergmann's rule? Ecography 9(4):285–293. https://doi.org/10.1111/j.1600-0587.1986.tb01221.x

Łomnicki A (1978) Individual differences between animals and the natural regulation of their numbers. J Anim Ecol 47(2):461–475. https://doi.org/10.2307/3794

Lorenzini R, Garofalo L, Qin X, Voloshina I, Lovari S (2014) Global phylogeography of the genus Capreolus (Artiodactyla: Cervidae), a Palaearctic meso-mammal. Zool J Linnean Soc 170(1):209–221. https://doi.org/10.1111/zoj.12091

Macdonald DW, Johnson PJ (2008) Sex ratio variation and mixed pairs in roe deer: evidence for control of sex allocation? Oecologia 158(2):361–370. https://doi.org/10.1007/s00442-008-1142-7

Matosiuk M, Borkowska A, Świsłocka M, Mirski P, Borowski Z, Krysiuk K, Danilkin AA, Zvychaynaya EY, Saveljev AP, Ratkiewicz M (2014) Unexpected population genetic structure of European roe deer in Poland: an invasion of the mtDNA genome from Siberian roe deer. Mol Ecol 23(10):2559–2572. https://doi.org/10.1111/mec.12745

Melis C, Jędrzejewska B, Apollonio M, Bartoń KA, Jędrzejewski W, Linnell JDC, Kojola I, Kusak J, Adamič M, Ciuti S, Delehan I, Dykyy I, Krapinec K, Mattioli L, Sagaydak A, Samchuk N, Schmidt K, Shkvyrya M, Sidorovich VE, Zawadzka B, Zhyla S (2009) Predation has a greater impact in less productive environments: variation in roe deer, Capreolus capreolus, population density across Europe. Glob Ecol Biogeogr 18(6):724–734. https://doi.org/10.1111/j.1466-8238.2009.00480.x

Muggeo VMR (2016) Testing with a nuisance parameter present only under the alternative: a score-based approach with application to segmented modelling. J Stat Comput Sim 86(15):3059–3067. https://doi.org/10.1080/00949655.2016.1149855

Mysterud A, Bartoń KA, Jędrzejewska B, Krasiński ZA, Niedziałkowska M, Kamler JF, Yoccoz NG, Stenseth NC (2007) Population ecology and conservation of endangered megafauna: the case of European bison in Białowieża Primeval Forest, Poland. Anim Conserv 10(1):77–87. https://doi.org/10.1111/j.1469-1795.2006.00075.x

Nilsen EB, Linnell JDC, Andersen R (2004) Individual access to preferred habitat affects fitness components in female roe deer Capreolus capreolus. J Anim Ecol 73(1):44–50. https://doi.org/10.1111/j.1365-2656.2004.00790.x

Nilsen EB, Gaillard JM, Andersen R, Odden J, Delorme D, Van Laere G, Linnell JD (2009) A slow life in hell or a fast life in heaven: demographic analyses of contrasting roe deer populations. J Anim Ecol 78(3):585–594. https://doi.org/10.1111/j.1365-2656.2009.01523.x

Olano-Marin J, Plis K, Sönnichsen L, Borowik T, Niedziałkowska M, Jędrzejewska B (2014) Weak population structure in European roe deer (Capreolus capreolus) and evidence of introgressive hybridization with Siberian roe deer (C. pygargus) in northeastern Poland. PLoS One 9(10):e109147. https://doi.org/10.1371/journal.pone.0109147

Pachkowski M, Cote SD, Festa-Bianchet M (2013) Spring-loaded reproduction: effects of body condition and population size on fertility in migratory caribou (Rangifer tarandus). Can J Zool 91(7):473–479. https://doi.org/10.1139/cjz-2012-0334

R Development Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Saether BE, Haagerund H (1985) Life history of the moose Alces alces: relationship between growth and reproduction. Ecography 8(2):100–106. https://doi.org/10.1111/j.1600-0587.1985.tb01159.x

Sand H, Cederlund G, Danell K (1995) Geographical and latitudinal variation in growth patterns and adult body size of Swedish moose (Alces alces). Oecologia 102(4):433–442. https://doi.org/10.1007/BF00341355

Servanty S, Gaillard JM, Toïgo C, Brandt S, Baubet E (2009) Pulsed resources and climate-induced variation in the reproductive traits of wild boar under high hunting pressure. J Anim Ecol 78:1278–1290

Simard MA, Coulson T, Gingras A, Cote SD (2014) Influence of density and climate on population dynamics of large herbivores under harsh environmental conditions. J Wildl Manag 74:1671–1685

Stewart KM, Bowyer RT, Dick BL, Johnson BK, Kie JG (2005) Density-dependent effects on physical condition and reproduction of American elk: an experimental test. Oecologia 143(1):85–93. https://doi.org/10.1007/s00442-004-1785-y

Strandgaard H (1972) An investigation of corpora lutea, embryonic development, and time of birth of roe deer (Capreolus capreolus) in Denmark. Dan Rev Game Biol 6:1–22

Tavecchia G, Coulson T, Morgan BJT, Pemberton JM, Pilkington JC, Gulland FMD, Clutton-Brock TH (2005) Predictors of reproductive cost in female Soay sheep. J Anim Ecol 74(2):201–213. https://doi.org/10.1111/j.1365-2656.2005.00916.x

Testa JW, Adams GP (1998) Body condition and adjustments to reproductive effort in female moose (Alces alces). J Mammal 79(4):1345–1354. https://doi.org/10.2307/1383026

Toïgo C, Gaillard JM, Van Laere G, Hewison AJM, Morellet N (2006) How does environmental variation influence body mass, body size, and body condition? Roe deer as a case study. Ecography 29(3):301–308. https://doi.org/10.1111/j.2006.0906-7590.04394.x

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York. https://doi.org/10.1007/978-0-387-87458-6