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1 The influence of birth date via body mass on individual  
2 fitness in a long-lived mammal

FLORIANE PLARD<sup>1,\*</sup>, JEAN-MICHEL GAILLARD<sup>1</sup>, TIM COULSON<sup>2</sup>, A.  
J. MARK HEWISON<sup>3</sup>, MATHIEU DOUHARD<sup>1</sup>, FRANÇOIS KLEIN<sup>4</sup>, DANIEL  
DELORME<sup>4</sup>, CLAUDE WARNANT<sup>4</sup>, AND CHRISTOPHE BONENFANT<sup>1</sup>

3 <sup>1</sup>*Université de Lyon, F-69000, Lyon; Université Lyon 1; CNRS, UMR5558, Laboratoire de  
Biométrie et Biologie Évolutive, F-69622, Villeurbanne, France.*

<sup>2</sup>*Department of Zoology, University of Oxford, The Tinbergen Building, South Parks Road,  
Oxford, OX1 3PS, United Kingdom*

<sup>3</sup>*INRA, UR035 CEFS, B.P. 52627, 31326 Castanet-Tolosan cedex, France*

<sup>4</sup>*Centre National d'Études et de Recherches Appliquées sur les Cervidés et Sanglier, Office  
National de la Chasse et de la Faune Sauvage, 85bis avenue de Wagram, 75017 Paris, France*

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\* Email: [floriane.plard@ens-lyon.fr](mailto:floriane.plard@ens-lyon.fr)

1           *Abstract.* The timing of birth has marked impacts on early life and early  
2 development of newborns in many species. Early-born offspring often survive and  
3 grow better than late-born offspring, but despite the long-lasting effects of early  
4 conditions on life history traits, the influence of birth date on fitness has rarely been  
5 investigated for long-lived species. In this study, we analyzed both the short- and  
6 long-term effects of birth date on individual life history traits and explored its  
7 subsequent impact on individual fitness in a population of roe deer. We considered  
8 both the direct effects, as well as the indirect effects of birth date mediated through  
9 the effects of body mass, on demographic parameters. We found that in addition to  
10 short-term effects on early body growth and survival, birth date generates “silver  
11 spoon” effects on adult life history traits of female roe deer. Birth date had  
12 long-lasting effects on female adult body mass such that early-born females were,  
13 on average, 3 kg heavier as adults than late-born females, although female adult  
14 survival was similar between these categories. Based on the observed relationships  
15 between birth date, body mass and demographic parameters, we built an integral  
16 projection model describing the simultaneous distributions of birth date and body  
17 mass to quantify the fitness consequences of birth date. We found that the fitness of  
18 early-born females was higher than that of late-born females. These long-lasting  
19 effects of birth date on fitness were mostly mediated through the influence of birth  
20 date on recruitment and adult body mass. By determining development of newborns  
21 during the early stages of life, birth date has a critical influence on each step of an  
22 individual’s subsequent life history trajectory.

23           *Key words:* silver spoon effect, life history traits, IPM, roe deer, body mass

INTRODUCTION

The timing of reproduction is critical in most species because it determines reproductive success of individuals (Price et al. 1988) and thus influences annual population growth. The timing of reproduction has been particularly well studied in the context of climate change (Dickey et al. 2008, Moyes et al. 2011) because a mismatch between birth timing and peak resource availability decreases annual recruitment (Post and Forchhammer 2008). At the population level, a high degree of birth synchrony may be the result of selection pressure on individuals to minimize this mismatch (Rutberg 1987) or, alternatively, be linked to a predator-swamping tactic (Estes 1976, Ims 1990). Indeed, in temperate areas, births are generally characterized by a high degree of seasonality and synchrony each year (Bronson 1989). However, within population variation in individual birth date has the potential to influence greatly early survival and body growth. Because body growth affects adult life history traits, birth date is expected to generate long-term effects on fitness (Lindström 1999, Cam and Aubry 2011). To date, most studies have focused on the short-term consequences of variation in individual birth date on the early stages of life, while evidence for long-term effects of birth date on adult life history stages and on fitness are lacking for long-lived species (Green and Rothstein 1993, Lindström 1999, Cam and Aubry 2011). In this paper, we thus investigated the long-term effects of individual birth date on adult life history traits and individual fitness. Yearly variation in weather conditions influences both the quality and the quantity of available resources during the period around birth. In temperate and northern areas, early-born young benefit from a longer growth period and attain a higher body mass before the onset of the harsh season than neonates born after the peak of vegetation production (moose *Alces alces*, Solberg et al. 2007, bighorn sheep, *Ovis canadensis* Feder et al. 2008). For example, in bighorn sheep, late-born lambs were 20% lighter in mid-September, at 3 months of age than lambs born one month earlier (Feder et al. 2008). For a given individual, being born early in the season also has

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1 positive effects on early survival in many species (red deer, *Cervus elaphus*, Guinness et al.  
 2 1978, western gulls, *Larus occidentalis*, Spear and Nur 1994, mosquitofish, *Gambusia affinis*,  
 3 Reznick et al. 2006). For instance, the probability of surviving until the end of the first winter  
 4 for red deer calves born very early was more than double that of calves born very late in the  
 5 season (Guinness et al. 1978). In some cases, young born very early in the season may  
 6 encounter harsh environmental conditions (Wilson et al. 2005) or suffer from higher predation  
 7 (Estes 1976) than young born during the peak of births. However, as a general rule, late-born  
 8 young have a lower early survival than individuals born early or during the birth peak in most  
 9 large herbivores and passerine birds.

10 Because it affects the early body development of young which, in turn, often determines  
 11 performance during adulthood (Douhard et al. 2013), date of birth has the potential to generate  
 12 long-term effects on adult phenotypic traits, but this question has seldom been investigated in  
 13 long-lived species. Indeed, a link between reproductive timing and fitness components has been  
 14 demonstrated for short-lived species (hatching date in lizard (Sinervo and Doughty 1996), birth  
 15 date in fish (Schultz 1993, Reznick et al. 2006) hatching date and fledging date in birds (Visser  
 16 and Verboven 1999, Sheldon et al. 2003, Saino et al. 2012) and birth date in small mammals  
 17 (Réale et al. 2003, Rödel et al. 2009)). However, the long-term effects of environmental  
 18 conditions in early life on adult life history traits are not universal (e.g., Wauters and Dhondt  
 19 1995 on European squirrels, Dobson et al. 1999 on Columbian ground squirrels) because some  
 20 individuals born in poor conditions can compensate for a bad start (Auer 2010 on guppies).  
 21 Nevertheless, poor early conditions may also permanently constrain body growth and generate  
 22 positive covariation among adult life history traits (the “silver spoon effect”, Grafen 1988) in  
 23 long-lived species. For instance, environmental conditions at birth influence both early survival  
 24 and growth (Gaillard et al. 2003, Landete-Castillejos et al. 2001, Beauplet et al. 2005), but also  
 25 adult life history traits such as body mass (roe deer, *Capreolus capreolus*, Pettorelli et al. 2002),  
 26 and lifetime reproductive success (red deer, Kruuk et al. 1999, oystercatchers, *Haematopus*

1 *ostralegus*, Van de Pol et al. 2006).

2 As a consequence of the long-term effects of early life conditions on life histories, females born  
 3 early should have high early survival and, when adult, could themselves give birth early in the  
 4 season. Because birth date and laying date have been found to be heritable (Réale et al. 2003,  
 5 Sheldon et al. 2003), the young of these early-born females should therefore also have high  
 6 early survival, so that early-born females should achieve higher fitness than late-born females.  
 7 Moreover, in species for which adult body mass is positively correlated with juvenile body  
 8 mass, females born early in the season should also be heavier, and so produce larger average  
 9 litter sizes, than late-born females. While such relationships are often assumed in studies using  
 10 laying (or birth) date as a proxy of female quality (Sydeman and Eddy 1995, Catry et al. 1999,  
 11 Blums et al. 2005), very few studies have explicitly investigated the relationship between  
 12 reproductive timing and individual fitness. In the present study, we defined individual fitness as  
 13 the individual reproductive value early in life (Moorad 2014, see also Methods for a justification  
 14 of this measure).

15 In this study, we investigated both the short-term and long-term effects of birth date on  
 16 individual life history traits and on fitness in an intensively monitored population of long-lived  
 17 mammals, roe deer. We tested the following hypotheses: (i) as predicted from the match  
 18 between early growth and resource availability (Rutberg 1987), early-born fawns should survive  
 19 better and have higher early body growth than late-born fawns because the former benefit from  
 20 high quality resources (Plard et al. 2014a), (ii) early-born individuals should be heavier when  
 21 adults, gain higher annual reproductive success, and live longer than late-born individuals  
 22 because early conditions have the potential to generate “silver spoon” effects (Grafen 1988).  
 23 Finally, using the observed relationships between birth date, body mass and demographic  
 24 parameters, we built an integral projection model (Easterling et al. 2000) to analyse the link  
 25 between birth date and fitness. We used an IPM (instead of a classical analysis of lifetime  
 26 reproductive success) for the following reasons: the IPM allowed us to estimate reproductive

1 value early in life for each birth date and to identify the exact pathways (i.e. survival,  
 2 reproduction, growth, or inheritance) by which birth date influences fitness. Moreover, by  
 3 building an IPM based on the distribution of two continuous traits, we could investigate both the  
 4 direct influence of birth date on fitness through its effect on annual reproductive success and  
 5 survival, as well as the indirect influence of birth date on fitness through its effect on body mass.  
 6 (iii) As long-lasting effects of early life often occur through permanent developmental  
 7 constraints (Lummaa and Clutton-Brock 2002), early-born individuals should achieve higher  
 8 fitness than late-born individuals, mainly because of the positive association between early birth  
 9 and fast body growth (e.g., Feder et al. 2008).

10 MATERIALS AND METHODS

11 *Study population*

12 The roe deer population at Trois Fontaines inhabits an enclosed 1,360ha forest in north-eastern  
 13 France (48°43'N, 2°61'W). The climate is continental, with relatively cold winters and warm  
 14 summers. This roe deer population has been intensively monitored since 1976 using a  
 15 Capture-Mark-Recapture (CMR) sampling design. Captured animals are individually marked  
 16 using collars (numbered or with VHF or GPS devices) and ear tags. The roe deer population at  
 17 Trois Fontaines is highly productive, mostly because of the rich habitats and soils which  
 18 promote high forest productivity (Pettorelli et al. 2006). Roe deer mate between mid-July and  
 19 mid-August. After copulation, embryos cease their development so that their implantation is  
 20 delayed by a five month diapause. Embryo development starts again in late December-early  
 21 January (Aitken 1974). Births in roe deer are highly seasonal, synchronous and occur from  
 22 mid-April to mid-June, with 80% of births taking place between the 5<sup>th</sup> and 27<sup>th</sup> of May at Trois  
 23 Fontaines (Gaillard et al. 1993). Birth dates are normally distributed, with a median birth date  
 24 of May 16<sup>th</sup>. Females are monoestrous and give birth to one, two, or occasionally three fawns



1 (triplets accounted for only about 2% of the litters), once per year, from 2 years of age onwards.

2 *Date of birth*

3 From the beginning of the birthing season (mid-April), a systematic search for fawns was  
 4 conducted every year from 1985 to 2012 by the Office National de la Chasse et de la Faune  
 5 Sauvage (Delorme et al. 1988). Between 21 and 63 newborn fawns were found each year  
 6 through either intensive searches performed by a line of people, or by directed searches targeted  
 7 towards the fawns of radio-collared females. Fawns were ear-tagged, weighed, sexed and aged  
 8 using umbilicus characteristics and behavior at marking (Jullien et al. 1992). Error when  
 9 estimating capture age is less than 2 days (Gaillard et al. 1993). Birth date was therefore  
 10 back-calculated based on the fawn's estimated age at the date it was found. Body mass at  
 11 capture did not allow us to estimate body mass at birth because early growth rates vary among  
 12 fawns. Roe deer fawns display a "hider" tactic (Lent 1974), only coming into close contact with  
 13 the mother for suckling. However, the mother stays in close proximity to its fawns, remaining  
 14 spatially isolated from other females. We relied on this behaviour to identify the fawn's mother  
 15 through direct observation of lactation behavior or by identification of an escaping female in the  
 16 vicinity of the fawn.

17 *Life history traits*

18 Winter captures of roe deer took place each year between January and mid-March. At each  
 19 capture, animals were weighed to the nearest 100g. Yearling and adult body masses  
 20 corresponded respectively to the body mass of a given female at 8 months old (i.e. at first winter  
 21 capture) and to its median mass as an adult between 4 and 10 years old (Pettorelli et al. 2002).  
 22 We assumed that the body mass of a given fawn at first capture measured between early January  
 23 and early March provides a reliable estimate of its body mass at 8 months of age because body  
 24 mass remains almost constant over the winter in roe deer (Hewison et al. 2002). The annual

1 reproductive success of each female was assessed by the capture of its marked fawns at 8  
 2 months old. As we did not have access to father-fawn filiations, and thus to male reproductive  
 3 success, we only included females for the analysis of the effect of birth date on adult stage  
 4 traits. The age of all reproducing females analyzed here was known exactly because they were  
 5 first captured either as newborns or at 8 months of age during their first winter (identified using  
 6 tooth eruption sequence, Flerov (1952)).

7 *Statistical analysis*

8 To investigate short- and long-term influences of birth date on female life history traits and  
 9 fitness, we considered both the direct effect of birth date on demographic parameters (survival,  
 10 reproduction) and the indirect effect of birth date on demographic parameters mediated through  
 11 its effect on body mass (see Fig. 1). Thus, we tested for both an effect of individual birth date  
 12 and of body mass (as a yearling or as an adult) on female adult body mass and annual survival.  
 13 For early life stage traits, we investigated the short-term influence of individual birth date on  
 14 early survival (survival from birth to 8 months old) and yearling survival, and yearling body  
 15 mass. In addition, as heavy mothers give birth earlier than light mothers in roe deer (Plard et al.  
 16 2014b), we considered the relationship between maternal body mass and early life history traits  
 17 of her offspring to control for possible maternal effects. Because these relationships included  
 18 information on both mother and newborn fawns, we included both male and female newborns  
 19 and corrected for sex when necessary to increase our sample size. There is no cost of being born  
 20 very early in the season in roe deer because the earliest born fawns have the highest early  
 21 survival (Plard et al. 2014a) and the highest yearling body mass, which is highly positively  
 22 correlated to yearling survival in ungulates (Gaillard et al. 2000b). We thus tested for the linear  
 23 effect of birth date on yearling and adult body masses, and on adult survival. Moreover, we have  
 24 previously shown that early survival is linked to birth date through a threshold relationship  
 25 (Plard et al. 2014a). As we expected a directional effect of body mass on life history traits, we

1 only tested for linear effects of body mass.

2 **Birth date and early life stage traits:** The influence of birth date and maternal body mass on  
 3 individual early survival (proportion of fawns of each litter that survived up to 8 months of age)  
 4 was investigated using a generalized linear mixed model with a logit link and a binomial  
 5 distribution. Because there is no difference between the sexes in individual early survival in roe  
 6 deer (mean survival difference: 0.13, SE: 0.25, p-value: 0.61, see also Gaillard et al. (1997)),  
 7 we pooled fawns of both sexes in this analysis. We modeled a threshold regression for birth date  
 8 (with constant survival until the 12<sup>th</sup> of May, then decreasing from this birth date onwards,  
 9 (Plard et al. 2014a)) and a linear regression for maternal body mass on individual early survival.  
 10 The influence of birth date and maternal body mass on yearling body mass was modeled using  
 11 linear mixed models. As males are heavier than females at 8 months of age in roe deer (Gaillard  
 12 et al. 1996), we included an effect of sex. In models describing individual early survival and  
 13 yearling body mass, we included cohort as a random effect on the intercept to control for  
 14 among-year variation in environmental conditions and maternal identity as a random effect to  
 15 control for the fact that among-female heterogeneity in reproductive performance is partly  
 16 unrelated to body mass and birth date. The influence of a female's birth date and yearling body  
 17 mass on its yearling survival (i.e. from 8 to 20 months old) was investigated using a generalized  
 18 linear mixed model, including cohort as a random effect.

19 **Birth date and adult stage traits:** To investigate whether individual birth date has a direct  
 20 effect on female adult body mass (over and above its indirect effect on adult body mass  
 21 mediated through its effect on individual yearling body mass), we performed a path analysis  
 22 (Shipley 2009). In all models, we included an influence of individual birth date on yearling  
 23 body mass and tested for direct effects of both individual birth date and yearling body mass on  
 24 individual adult body mass using a linear model, including only females. The influence of a  
 25 female's birth date and adult body mass on its adult survival was tested using a  
 26 capture-mark-recapture (CMR) framework. Models were fitted using capture histories of 110

1 females in the software ESURGE (Choquet et al. 2009). Based on previous studies in this  
 2 population (e.g., Choquet et al. 2011), recapture probability was modeled for 3 discrete time  
 3 periods (1986-1999, 2000, 2001-2012).  
 4 For each life history trait except adult body mass, the best model was selected using the Akaike  
 5 Information Criterion (AIC, Burnham and Anderson 2002). We selected the model with the  
 6 lowest AIC and highest AIC weight ( $w_i$ , calculated as a measure of the likelihood that a given  
 7 candidate model is the best among the set of fitted models). For modeling adult body mass, we  
 8 used a path analysis in a Bayesian framework (Gelman and Hill 2007) with OpenBUGS and  
 9 tested for both the influence of yearling body mass and for the direct effect of individual birth  
 10 date on adult body mass using the Deviance Information Criterion (DIC, following Gelman and  
 11 Hill 2007, see also Spiegelhalter et al. 2002). We conducted 20000 simulations and used the  
 12 first 5000 as burn-in. We checked that the parameters estimated from the models we fitted were  
 13 not influenced by multi-collinearity problems (especially between birth date and body mass). We  
 14 compared the values of body mass and birth date estimated from models with and without body  
 15 mass and birth date included. Estimates were similar in all models. Diagnostic plots displaying  
 16 the residuals of each selected model are presented in the supplementary material (Fig. A3 and  
 17 A4).

18 **Birth date and individual fitness.** To investigate the influence of birth date on fitness  
 19 (measured using reproductive value early in life), we used an integral projection model (IPM) to  
 20 analyse the dynamics of the distributions of two continuous traits over time (Easterling et al.  
 21 2000, Ellner and Rees 2006, Coulson 2012): body mass ( $bm$ ) and birth date ( $bd$ ), for female roe  
 22 deer in the population of Trois Fontaines. The contemporaneous distributions of body mass and  
 23 birth date at year  $t + 1$  according to their age  $a + 1$  (the proportion of individuals of age  $a + 1$   
 24 and class ( $bm, bd$ ) at year  $t + 1$  in the population is defined by  $n(a + 1, t + 1, bm, bd)$ ) depend  
 25 on their distributions at year  $t$  and on five functions: (1) the *inheritance function for birth date*  
 26 ( $\mathbf{I}_{bd}(a, t, bm, bd' | bd)$ ) links the offspring's birth date to the birth date and body mass of the

1 mother. Following standard terminology in the IPM literature (Coulson et al. 2011, Coulson  
 2 2012), we defined inheritance as the part of the trait that is transmitted from mothers to  
 3 offspring, irrespective of the mechanism of transmission. This measure includes all  
 4 environmental sources of similarity (e.g., maternal effects, common habitat effects, permanent  
 5 environment effects) and, is equivalent to “inclusive heritability” (sensu Danchin et al. 2011).  
 6 (2) The *recruitment function* ( $\mathbf{R}(a, t, bm, bd')$ ) describes the number of offspring a mother  
 7 successfully raised as a function of their birth date and the mother’s body mass. (3) The  
 8 *inheritance function for body mass* ( $\mathbf{I}_{bm}(a, t, bm'|bm, bd')$ ) links an offspring’s body mass at 8  
 9 months of age (yearling body mass) to its birth date and maternal body mass. (4) The *growth*  
 10 *function* ( $\mathbf{G}(a, t, bm'|bm, bd)$ ) describes the individual-level relationship between body mass as  
 11 a yearling and body mass as an adult, given that individual’s birth date. As birth date is unique  
 12 for a given individual, the growth function included also an implicit developmental function for  
 13 birth date defined as an identity function. Finally, (5) the *survival function* ( $\mathbf{S}(a, t, bm, bd)$ )  
 14 describes the probability that an individual survives in relation to its birth date and body mass.

15 Then:

$$16 \mathbf{n}(1, t+1, bm', bd') = \sum_a \int \int \mathbf{I}_{bm}(a, t, bm'|bm, bd') \mathbf{R}(a, t, bm, bd') \mathbf{I}_{bd}(a, t, bm, bd'|bd) \mathbf{n}(a, t, bm, bd) dbm dbd$$

$$17 \mathbf{n}(a+1, t+1, bm', bd) = \int \int \mathbf{G}(a, t, bm'|bm, bd) \mathbf{S}(a, t, bm, bd) \mathbf{n}(a, t, bm, bd) dbm dbd, a \geq 1$$

18 The continuous IPM can be approximated as a high dimensional discrete matrix (Easterling  
 19 et al. 2000, see also supplementary material, Fig. B2). To minimize the size of the matrix, we  
 20 used a two age-class structure: yearling (1 year old) and adult females (Nilsen et al. 2009),  
 21 illustrated in the Fig. B1. As adult body mass of an individual female varies little among years  
 22 in roe deer (e.g. Andersen et al. 2000, Plard et al. 2014b), we assumed that an individual’s body  
 23 mass was constant from 2 years old to death and equal to its median adult body mass (between  
 24 4 and 10 years old), so limiting the size of the matrix to two age classes. While this assumption  
 25 may lead to a slight over-estimate of body mass for 2 and 3 year old individuals and for females  
 26 older than 10 years old, this is unlikely to overly influence our analyses. Roe deer females

1 indeed reach 93% of their adult body mass at 2 years of age and body mass of senescent  
 2 females is 96% of their adult body mass (a decrease of 1 kg on average, Hewison et al. 2011).  
 3 All functions required to build the IPM were investigated in the previous analyses (i.e. on birth  
 4 date and early life stage traits and on birth date and adult stage traits) except the inheritance  
 5 function for birth date. We thus used the parameters (intercepts and slopes) previously  
 6 estimated from the selected models of early and adult life history traits (Table B1, Fig. 1) for the  
 7 survival, growth, inheritance for body mass and recruitment functions and investigated the  
 8 effects of maternal birth date and body mass on the inheritance function for birth date to build  
 9 the IPM. For the inheritance function for birth date, we modeled the link between offspring  
 10 birth date and maternal birth date and body mass using a linear mixed model, including year  
 11 and maternal identity as random effects on the intercept. Sex was not included as there is no  
 12 difference in average birth date between male and female roe deer (Gaillard et al. 1993).  
 13 As almost all roe deer females give birth to two fawns in the studied population (Gaillard et al.  
 14 1998), we considered litter size at birth as a fixed parameter and modeled the *recruitment*  
 15 *function* based solely on estimates of early survival from birth to the onset of winter (at 8  
 16 months of age). As the sex ratio at birth of roe deer is close to 0.5 (Hewison et al. 1999), litter  
 17 size at birth was set to one as only females were considered in the IPM. We modeled both the  
 18 *inheritance* and the *growth functions* using a normal probability density. The mean of each of  
 19 these functions provides the link between the offspring trait and the maternal trait (including the  
 20 effect of the individual's birth date for the inheritance function for body mass) for the  
 21 inheritance functions and between an individual's adult body mass and its yearling body mass  
 22 and its birth date for the growth function. The variances of these functions were estimated from  
 23 the squared residuals of the mean relationships and were kept constant.  
 24 We quantified the influence of birth date on fitness by estimating the individual reproductive  
 25 value of roe deer at 8 months of age in relation to their birth date. Reproductive value was first  
 26 introduced by Fisher (1930) to measure the extent to which individuals of different ages

1 contribute to future population growth. For a large population living in a constant environment,  
 2 the sum of the reproductive values over all individuals is proportional to the exponential growth  
 3 rate  $r$  (i.e. Malthusian growth rate) of the population irrespective of its age distribution (Fisher  
 4 1930, Engen et al. 2009). For instance, reproductive values were recently used as a metric of  
 5 fitness in different contexts (see e.g. Engen et al. 2009; 2012, Bouwhuis et al. 2012). Moreover,  
 6 assuming that the population growth rate is constant, reproductive value at birth measures  
 7 individual fitness (Moorad 2014). We therefore chose reproductive value in early life to  
 8 measure fitness and not the more commonly used asymptotic population growth rate ( $r$ )  
 9 (Caswell 2001). Indeed, the life cycle of roe deer used in our analysis (Fig B1) corresponds  
 10 precisely to the model where maximizing reproductive value is equivalent to maximizing fitness  
 11 (Caswell 2001). Moreover, using an integral projection model allowed us to generate a given  
 12 reproductive value for each birth date class, whereas we had only one asymptotic population  
 13 growth rate for the entire population. As noted by Fisher himself,  $r$  is the average individual  
 14 fitness and is therefore a property of the population. This measure can be biased when used at  
 15 the individual level because the average of individual measures (individual  $r$ ) is not equal to the  
 16 asymptotic population growth rate. Moreover, in contrast to other commonly used measures of  
 17 individual fitness like lifetime reproductive success (Clutton-Brock 1988, Newton 1989),  
 18 reproductive values account for how much a given heritable genotype will contribute to future  
 19 generations (Maciejewski 2014) and for the timing of reproduction. In long-lived species for  
 20 instance, two individuals that successfully raised the same number of offspring during their  
 21 lifetime, but at different ages, have the same lifetime reproductive success but different  
 22 reproductive values when population growth differs from 0.

23 Given the available data, we estimated reproductive values at 8 months of age rather than at birth  
 24 as commonly done. Indeed, we did not have measures of body mass at birth for most individuals  
 25 monitored, which were first weighed at 8 months of age and recruited then in our demographic  
 26 model (see the definition of the recruitment function). We approximated reproductive values at

1 birth as the reproductive values at 8 months, which means that we underestimated the influence  
 2 of birth date on fitness by not accounting for the influence of birth date on early survival (Plard  
 3 et al. 2014a). To estimate the confidence interval of the individual reproductive values, we  
 4 performed a bootstrap analysis with 2000 simulations of the datasets used to estimate the  
 5 different functions of the IPM (except for adult survival that remained constant with respect to  
 6 body mass and birth date, see results). Second, to investigate the relative influence of each  
 7 function on the difference in fitness between early- and late-born individuals, we performed a  
 8 perturbation analysis. We estimated the percentage change in the difference in fitness between  
 9 early- and late-born females after a 1% change of one of the slopes linking birth date and body  
 10 mass to the vital rates. Finally, we simulated 60 groups of 1000 yearling females which differed  
 11 in terms of their birth date and that were monitored until the death for all individuals in the  
 12 group. For each group, we recorded mean adult body mass, annual reproductive success, and  
 13 both mean female offspring body mass and life expectancy at 8 months of age as predicted by  
 14 the IPM. All statistical analyses were performed with the R software from codes (available in  
 15 the supplemental material) that we wrote based on Easterling et al. (2000) and Coulson (2012).

16 RESULTS

17 *Birth date and early life stage traits*

18 Early survival of individual fawns was best described by a model that included additive effects  
 19 of individual birth date and maternal body mass (Table 1A,  $w_i = 0.67$ , N=256 including 120  
 20 different mothers with 2.1 repetitions per mother on average). Fawns born before 12<sup>th</sup> May had  
 21 a probability of 0.52 [0.42;0.61], on average, of surviving to 8 months old. Early survival  
 22 probability decreased from this date onwards such that fawns born late in the season (May, 31<sup>st</sup>,  
 23 Fig. 2A) had a probability of only 0.32 [0.20;0.48], on average, of surviving to the same age  
 24 (Table A1A and Fig. 2A). Maternal body mass influenced early survival positively (Table A1A)



1 such that fawns born to mothers weighing 20 kg had, on average a 0.25 [0.14;0.40] probability  
 2 of surviving, while those born to mothers weighing 28 kg had, on average, a 0.71 [0.54;0.83]  
 3 probability of surviving (for fawns born at the peak of the birth season). This model accounted  
 4 for 6% (of which, 1% was due to the effect of birth date) of the observed variation in early  
 5 survival (note that the proportion of variation explained for a binomial response variable is  
 6 always much lower than that for a Gaussian variable).

7 Individual yearling body mass was best described by a model that included additive effects of  
 8 maternal body mass and individual birth date (Table 1B,  $w_i = 0.98$ , N=111 including 67  
 9 different mothers with 1.6 repetitions per mother on average) and which explained 26% (of  
 10 which, 9% was due to the effect of birth date) of the observed variation in yearling body mass.  
 11 Early-born fawns (1<sup>st</sup> May) were 2.9 kg (20%) [1;4.9 kg] heavier, on average, at 8 months of  
 12 age than late-born fawns (31<sup>st</sup> May) (Table A1B and Fig. 2B). Moreover, for a given birth date,  
 13 heavy mothers (28 kg) produced offspring that were, on average, 3.1 kg (21.5%) [0.6;5.6 kg]  
 14 heavier at 8 months of age than light (20 kg) mothers. Nevertheless, our diagnostic plot (Fig.  
 15 A3) showed that the residuals of the regression tended to increase with the fitted values. This  
 16 trend was directly linked to the random individual (maternal) effect, suggesting that an  
 17 unidentified variable related to a maternal effect could influence the inheritance of body mass.  
 18 The best model describing individual yearling survival from 1 to 2 years of age included an  
 19 effect of individual yearling body mass (Table 1C,  $w_i = 0.44$ , N=113). Heavier yearlings had a  
 20 higher probability of surviving to 2 years of age than lighter yearlings (0.89 vs. 0.99 for  
 21 yearlings of 12 kg and 20 kg, respectively, Fig. A4). Adding birth date did not improve the  
 22 model fit, which indicates that birth date has no detectable effect on yearling survival.

23 *Birth date and adult stage traits*

24 The best model describing individual adult body mass included additive effects of birth date  
 25 together with the indirect effect of birth date on adult body mass mediated through yearling

1 body mass (Table 1D, N=67). The retained model accounted for 50% of the observed variation  
 2 in adult body mass, of which 6% was explained by the direct effect of individual birth date  
 3 (Table A1D). Whether or not we included the two individuals with an adult body mass of 18 kg  
 4 that appear as outliers in Fig. 3 had no influence on model selection or parameter estimates.  
 5 When considering only the direct effect of birth date on adult body mass, early-born individuals  
 6 (1<sup>st</sup> May) reached a body mass that was 6.5% higher than late-born individuals (31<sup>st</sup> May)  
 7 (24.0 kg vs. 22.5 kg, Fig. 3). However, individual birth date influenced adult body mass mainly  
 8 through its effect on yearling body mass which was a better predictor of adult body mass than  
 9 birth date ( $\Delta DIC = 40.6$  if we removed the effect of yearling body mass from the best model  
 10 vs.  $\Delta DIC = 1.4$  if we removed the effect of birth date from the best model, Table 1D). A  
 11 yearling weighing 12 kg reached an adult body mass of, on average, 20.8 kg, whereas a yearling  
 12 weighing 20 kg weighed, on average, 25.8 kg as an adult.  
 13 As effects of female birth date or body mass on individual adult survival were non-significant  
 14 (Table 1E, Table A1E, N=110), we used all monitored females to estimate an overall adult  
 15 survival probability (N=418). The annual survival rate of adult females was 0.824 [0.796;0.850]  
 16 (Fig. A1).

17 *Birth date and fitness*

18 We built an IPM from the parameter estimates that we generated above for each function (Table  
 19 B1). For the inheritance function for birth date, offspring birth date was positively related to  
 20 maternal birth date (Table A2,  $w_i = 0.35$ , N=89 including 33 different mothers with 2.7  
 21 repetitions per mother on average) such that females born early in the season (1<sup>st</sup> May) gave  
 22 birth, on average, 5 [-2;13] days earlier than females born late (31<sup>st</sup> May) in the season (Fig.  
 23 A2). Five per cent of the observed variation in offspring birth date was explained by this model.  
 24 The diagnostic plot of this model showed a trend between the residuals and the fitted values  
 25 (Fig. A3), probably for the same reason as the trend observed in the diagnostic plot of the

1 model for the inheritance function for body mass.

2 We evaluated the stable distribution of body mass and birth date from the right eigenvector of

3 the projection matrix. The stable distribution of body mass revealed two peaks corresponding to

4 a mean body mass of 16 kg and 23 kg for yearling and adult female roe deer, respectively (Fig.

5 C1A). The stable distribution of yearling birth dates was also in agreement with field

6 observations, with a mean birth date of 135.5 (15-16<sup>th</sup> May vs. 16<sup>th</sup> May for the observed mean

7 birth date of newborns in this population) and a normal distribution of birth dates (Fig. C1B).

8 Using this IPM allowed us to estimate reproductive value at 8 months of age, and thereby

9 fitness, of females in relation to their birth date (Fig. C2). We report here the relative change in

10 reproductive value (and not absolute estimations of reproductive value) between early- and

11 late-born individuals because reproductive values should be interpreted as relative values. We

12 estimated that the fitness of early-born females (1<sup>st</sup> May) was 1.29 (95% confidence interval:

13 [1.01 3.47]) higher than that of late-born females (31<sup>st</sup> May). The perturbation analysis showed

14 that birth date had both a direct effect (on early survival and inheritance) and an indirect effect

15 (through body mass) on fitness (Fig. 4). Indeed, the difference in fitness between early- and

16 late-born individuals was closely related to the slopes linking birth date to early survival (when

17 we decreased the slope of the recruitment function for birth date by 1%, the difference in fitness

18 between early- and late born females increased by 0.61%) and linking maternal birth date to

19 offspring birth date (a 1% change in the slope of the inheritance function for birth date led to a

20 0.40% change in the difference in fitness). This difference was also closely related to the

21 indirect effect of birth date on fitness mediated through body mass. Indeed, a 1% change in the

22 slope of the growth function for birth date and in the inheritance function for body mass led to a

23 0.35% and to a 0.21% change in the difference in fitness between early- and late-born females,

24 respectively. Simulating 60 groups of yearlings born on different days indicated that early-born

25 females (1<sup>st</sup> May) weighed 3.3 kg (13%) more as adults than late-born females (31<sup>st</sup> May).

26 Moreover a 1% change in the slopes linking body mass and the vital rates led to a change in the

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1 difference in fitness between early- and late-born females of 0.50% for recruitment, 0.38% for  
 2 growth and 0.07% for the inheritance function for body mass. Only the survival function  
 3 contributed relatively little to the difference in fitness between early- and late-born females (Fig.  
 4 4). Because birth date had no statistically significant direct effects on survival but was weakly  
 5 related to yearling survival through its effect on yearling body mass, life expectancy at 8 months  
 6 of age was slightly higher for early-born individuals than for late-born individuals (6.57 +/- 4.91  
 7 vs. 6.41 +/-4.93).

8 DISCUSSION

9 Using the relationships between birth date, body mass and early and late life history traits, we  
 10 built an IPM that allowed us to estimate the difference in fitness between early- and late-born  
 11 females. The fitness of early-born individuals was 1.3 higher than that of late-born individuals.  
 12 While the importance of variation in birth timing for life histories has been acknowledged for a  
 13 long time (Bronson 1989, Lindström 1999), the few studies demonstrating long-lasting effects  
 14 of birth date in mammals are recent and confined to short-lived species (e.g. European rabbit  
 15 *Oryctolagus cuniculus*, Rödel et al. 2009). Indeed, Wilson et al. (2005) found no evidence for  
 16 direct effects of birth timing on fitness in the Soay sheep (*Ovis aries*), the only moderately  
 17 long-lived mammal studied so far. Our results in a wild population of roe deer suggest that the  
 18 timing of birth can have a strong long-term influence on life histories, even in long-lived species.  
 19 Building an IPM based on the distribution of two contemporaneous traits allowed us to identify  
 20 the relative contribution of each function (i.e. survival, recruitment, growth, and inheritance) to  
 21 the difference in fitness observed between early- and late-born individuals. We found that the  
 22 silver spoon effect of birth date in roe deer is generated by both the direct effect of birth date on  
 23 recruitment and by the indirect effect of birth date on the different vital rates through body  
 24 mass. The indirect effect of birth date on fitness through body mass is a crucial pathway,  
 25 because the higher body mass that early-born fawns attained when adult mostly accounts for

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1 their higher fitness. Body mass has a strong influence on reproduction in large herbivores and is  
 2 often directly linked to individual quality (Gaillard et al. 2000a, Hamel et al. 2009). As a  
 3 consequence, compared to body mass, birth date per se only has a minor impact on the  
 4 demography of the studied roe deer population. An IPM based on body mass only (i.e. without  
 5 including birth date) would provide a reliable picture of the dynamics of this population but  
 6 would not provide a mechanistic understanding of the influence of birth date on fitness. The  
 7 IPM including both birth date and mass highlighted two key findings: (1) birth date plays a  
 8 determinant role in shaping individual fitness, with early-born females enjoying higher fitness  
 9 than late-born ones, and (2) the influence of birth date is mostly indirect, with the main pathway  
 10 involving changes in body mass.

11 Birth date commonly affects early life history traits in many species (Guinness et al. 1978,  
 12 Reznick et al. 2006, Feder et al. 2008, Solberg et al. 2007), including roe deer. Indeed, we  
 13 found that birth date had a marked influence on early survival, with early-born fawns surviving  
 14 much better than late-born individuals. Early-born fawns also reach a higher body mass as  
 15 yearlings than late-born individuals. These short-term effects of birth date probably result from  
 16 the high food quality available in early spring. The nutritional value of plants is high at the  
 17 beginning of the growing season and decreases as they mature (Klein 1965, Albon and  
 18 Langvatn 1992). Thus, early-born fawns have access to high quality milk, and in large  
 19 quantities, from their mothers who have access to plentiful, highly digestible food resources. As  
 20 a consequence, they reach a higher body mass as yearlings than late-born individuals.

21 Long-lasting impacts of environmental conditions at birth have often been supposed to be  
 22 mediated through early development (Lindström 1999, Kruuk et al. 1999). For instance,  
 23 environmental conditions at birth affect both early and late body growth in male and female roe  
 24 deer in two populations (Douhard et al. 2013). Similarly, birth date influences fitness of female  
 25 roe deer through long-lasting effects on both juvenile and adult body masses in one of these  
 26 populations. The indirect effect of birth date on adult body mass through yearling body mass is

1 clearly related to the match between birth timing and food resource availability. Fawns of  
 2 temperate areas that are born early grow for a longer time during the plant growing season and  
 3 so survive better. The biological interpretation of the direct influence of birth date on adult body  
 4 mass is more challenging, but the establishment of permanent physiological and metabolic  
 5 functions during gestation and very early life could explain the direct effect of early conditions  
 6 on adult life history traits (Lummaa and Clutton-Brock 2002). In particular, the development of  
 7 muscle tissue up until the adult stage is linked to fetal and very early life conditions, because the  
 8 number of muscle fibers is fixed at birth and strongly influenced by maternal nutrition (Du et al.  
 9 2010). Moreover, although natal dispersal is quite frequent in roe deer of both sexes (Gaillard  
 10 et al. 2008, Debeffe et al. 2012), many fawns remain philopatric and settle on a home range that  
 11 is contiguous or overlapping with their maternal home range (Strandgaard 1972). An alternative  
 12 explanation for the direct effect involves the correlation between individual quality and habitat  
 13 quality, which could thus at least partly explain the direct influence of early life on adult body  
 14 mass. Our results contrast with those on Soay sheep where no direct influence of birth date on  
 15 fitness was detected and the long-lasting effect of birth date was simply linked to birth mass  
 16 (Wilson et al. 2005). The markedly fluctuating environmental conditions faced by the Soay  
 17 sheep population (Coulson 2001) have a strong influence on annual body mass and could mask  
 18 any direct long-term effect of birth date on fitness.

19 The influence of birth timing on adult life history traits has been intensively studied in birds. In  
 20 the intensively studied barn swallow, a short-lived species (< 6 years in this study), hatching  
 21 date was negatively associated with lifetime reproductive success (Saino et al. 2012). However,  
 22 the biological link between reproductive timing and fitness differs between barn swallows and  
 23 roe deer. In barn swallows, early hatched individuals are longer-lived than late hatched birds  
 24 and thereby obtain higher lifetime reproductive success through a greater number of  
 25 reproductive attempts. In contrast, in roe deer, we have shown that birth date has no effect on  
 26 adult survival which, as a general rule, varies little among years in large mammals (Gaillard

1 et al. 2000b, Gaillard and Yoccoz 2003). In roe deer, birth timing-related fitness differences  
 2 among individuals arise because of variation in annual reproductive success rather than in  
 3 reproductive lifespan. This difference in reproductive performance is likely linked to the 3 kg  
 4 higher adult body mass of early-born females compared to late-born females. Thus, early-born  
 5 females are more successful in raising their offspring (Andersen et al. 2000).  
 6 Females which are born the earliest, which are also the heaviest and attain the highest fitness,  
 7 can be considered as the highest quality individuals (Hamel et al. 2009). Indeed, while a variety  
 8 of mechanisms may link birth or hatching date to fitness, birth date can be considered as an  
 9 important component of the multi-dimensional complex that describes individual quality (sensu  
 10 Wilson and Nussey 2010). In roe deer, we have shown that birth date influences the whole life  
 11 history trajectory of an individual. Nonetheless, one cannot predict an individual's trajectory  
 12 from its birth date alone. Individual life history trajectories are shaped by both early  
 13 environmental conditions (including birth date) and current environmental conditions  
 14 (Tuljapurkar et al. 2009). The relative role of traits that are fixed at birth, such as maternal home  
 15 range or environmental conditions at birth, versus traits that vary across an individual's lifetime  
 16 in response to dynamic environmental variations remains to be quantified (Tuljapurkar et al.  
 17 2009, but see Helle et al. 2012 on the bank vole). In our models including both early and late life  
 18 history traits, birth date explained a maximum of 9% of the observed variation in the life history  
 19 traits that we studied. The large amount of unexplained variation in these life history traits can  
 20 be assumed to be linked to either annual environmental conditions or stochastic variation.  
 21 Yearly variation in environmental conditions affects annual body condition (McNamara and  
 22 Houston 1996) and the environmental cues used by different species to time their reproduction  
 23 (Reed et al. 2010). In a species like roe deer that displays little among-year variation in body  
 24 mass, body condition (Andersen et al. 2000) or timing of birth (Plard et al. 2013), we expect  
 25 that birth date and early life conditions would markedly influence individual life history  
 26 trajectories. On the contrary, in a species that shows large among-year variation in annual body

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1 condition (bighorn sheep, Festa-Bianchet 1998) or in species with marked phenotypic plasticity  
 2 (such as the great tit, *Parus major*, Nussey et al. 2005), the relative influence of current annual  
 3 environmental conditions on life history trajectories should be higher than in roe deer.  
 4 Consequently, the magnitude of the long-lasting effects of early conditions for shaping  
 5 individual life history trajectories and population dynamics is likely to vary as a function of the  
 6 life history strategy of the species.

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SUPPLEMENTAL MATERIAL

**Appendix A**

Description of the model describing the early life stage and adult stage traits in roe deer including the parameter estimates of the different models, the plots of the survival and the inheritance function for birth date and, the diagnostic plots of the different models.

**Appendix B**

Description of the different functions and of the matrix used to build the IPM.

**Appendix C**

Description of the outputs (stable birth date and body mass distributions and, reproductive values) of the IPM.

**Supplement**

R script used to build the IPM.

1 **Table 1.** Model selection for the early life stage and adult stage traits. **A. Early survival**  
 2 **(Recruitment function of the IPM).** Influence of maternal body mass ( $BM_M$ ) and individual  
 3 birth date ( $BD$ , with a threshold date on May 12<sup>th</sup>) on individual early survival (to 8 months of  
 4 age). **B. Yearling body mass (Inheritance function for body mass).** Influence of individual  
 5 birth date ( $BD$ ) and of maternal body mass ( $BM_M$ ) on individual yearling body mass. An  
 6 effect of sex was included in the models because yearling males are heavier than yearling  
 7 females. **C. Yearling survival.** Influence of individual birth date ( $BD$ ) and yearling body mass  
 8 ( $BM_Y$ ) on individual yearling survival ( $Y$ ). **D. Adult body mass (Growth).** Influence of  
 9 individual birth date ( $BD$ ) and yearling body mass ( $BM_Y$ ) on female adult body mass. An  
 10 indirect effect of birth date on adult body mass through its effect on yearling body mass was  
 11 also included in all models using a path analysis. **E. Adult survival.** Influence of individual  
 12 birth date ( $BD$ ) and adult body mass ( $BM_{Ad}$ ) on female adult survival.  $k$  indicates the number  
 13 of estimated parameters, LL is the maximum log likelihood, Dev is the deviance of the model,  
 14  $\Delta AIC$  indicates the difference in the AIC between two competing models, and  $w_i$  corresponds  
 15 to Akaike weights.  $Pd$  is the estimated number of parameters,  $\hat{D}$  is the deviance of the model  
 16 and  $\Delta DIC$  indicates the difference in the DIC between two competing models. The selected  
 17 models are indicated in bold. 1 represents the constant model (i.e. intercept only).

TABLE 1.

Early life stage traits				
<b>A. early survival</b>				
	<i>k</i>	LL	$\Delta$ AIC	<i>w<sub>i</sub></i>
<b><i>BM<sub>M</sub> + BD</i></b>	<b>5</b>	<b>-181.347</b>	<b>0</b>	<b>0.673</b>
<i>BD</i>	4	-185.941	7.187	0.018
<i>BM<sub>M</sub></i>	4	-183.140	1.585	0.304
1	3	-188.334	9.975	0.005
<b>B. yearling body mass</b>				
	<i>k</i>	LL	$\Delta$ AIC	<i>w<sub>i</sub></i>
<b><i>sex + BM<sub>M</sub> + BD</i></b>	<b>7</b>	<b>-238.091</b>	<b>0</b>	<b>0.970</b>
<i>sex + BD</i>	6	-242.601	7.021	0.029
<i>sex + BM<sub>M</sub></i>	6	-246.0224	13.863	0.001
<i>sex</i>	5	-250.932	21.682	$\leq 0.001$
<b>C. yearling survival</b>				
	<i>k</i>	LL	$\Delta$ AIC	<i>w<sub>i</sub></i>
<b><i>BM<sub>Y</sub> + BD</i></b>	<b>4</b>	<b>-20.757</b>	<b>0.488</b>	<b>0.345</b>
<b><i>BM<sub>Y</sub></i></b>	<b>3</b>	<b>-21.513</b>	<b>0</b>	<b>0.441</b>
<i>BD</i>	3	-22.875	2.724	0.113
1	2	-23.980	2.934	0.102
Adult stage traits				
<b>D. adult body mass</b>				
	<i>P<sub>d</sub></i>	$\hat{D}$	$\Delta$ DIC	
<b><i>BM<sub>Y</sub> + BD</i></b>	<b>7</b>	<b>537.400</b>	<b>0</b>	
<i>BM<sub>Y</sub></i>	6	540.900	1.400	
<i>BD</i>	6	580.300	40.600	
1	5	585.300	43.500	
<b>E. adult survival</b>				
	<i>k</i>	Dev	$\Delta$ AIC	<i>w<sub>i</sub></i>
<b><i>BM<sub>Ad</sub> + BD</i></b>	<b>7</b>	<b>1462.309</b>	<b>3.733</b>	<b>0.080</b>
<i>BM<sub>Ad</sub></i>	6	1462.531	2.055	0.185
<i>BD</i>	6	1462.323	1.746	0.216
<b>1</b>	<b>5</b>	<b>1462.576</b>	<b>0</b>	<b>0.518</b>

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FIGURE CAPTION

**Figure 1.** Conceptual model of the relationships among life history traits used to build the five functions of the IPM: the inheritance function for birth date, the inheritance function for body mass, the recruitment, the growth and the survival functions. Dotted arrows indicate potential effects that were not supported by the selected model.

**Figure 2.** Influence of individual birth date on individual early survival (A.) and yearling body mass (B.) for roe deer at Trois Fontaines, France. (A.) Data used to fit the model are represented by filled circles whose size is proportional to the number of observed births within 25 classes of birth date (of 2 days from April 17<sup>th</sup> to June 5<sup>th</sup>). Males and females were pooled in this analysis (B.) Partial residuals of observed yearling body mass (corrected for maternal body mass and sex) are presented. Males and females are presented in black and grey, respectively, with one point representing one individual. The predictions of the model with their 95% confidence intervals are presented with a grey shade .

**Figure 3.** Long-term direct and indirect (i.e. mediated through body mass) influence of individual birth date on individual adult body mass for female roe deer at Trois Fontaines, France. The dotted line gives the predictions of the direct effect of birth date, only.

**Figure 4.** Percentage change of the difference in fitness between early- and late-born female roe deer generated by a 1% change in the slopes of each function (Rec: Recruitment, Inh\_bd: Inheritance for birth date, Inh\_bm: Inheritance for body mass, Gro: Growth and Sur:survival). Perturbations of slopes linking birth date and body mass to the early and adult life history traits are presented in black and white, respectively.

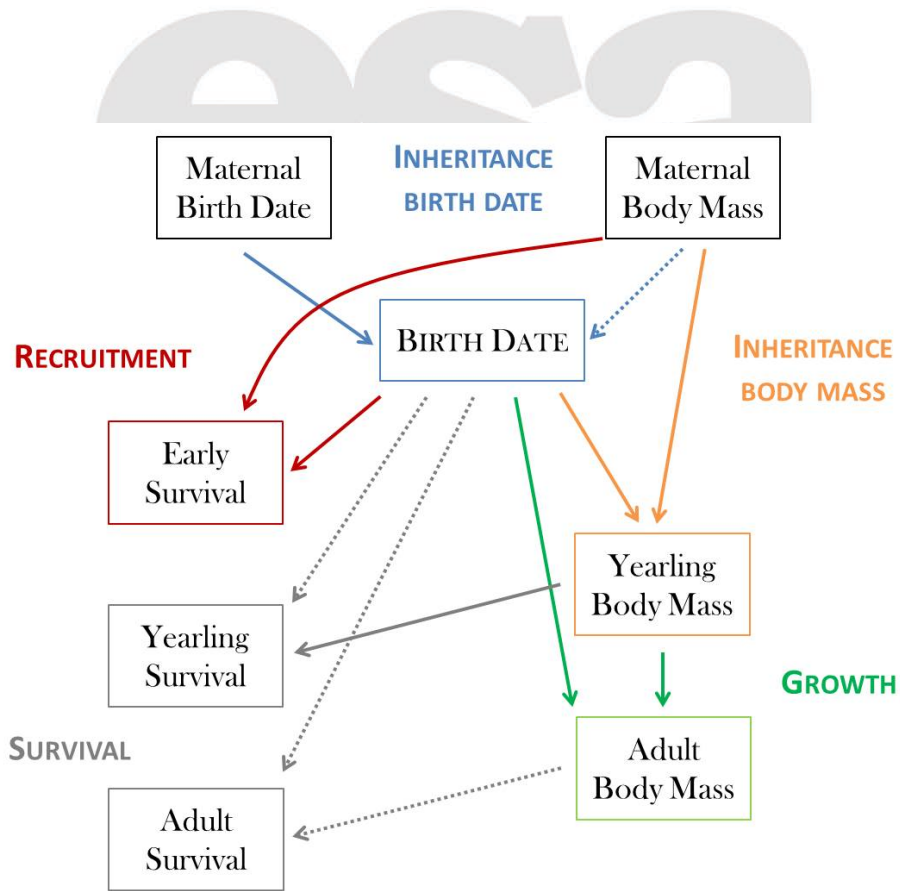
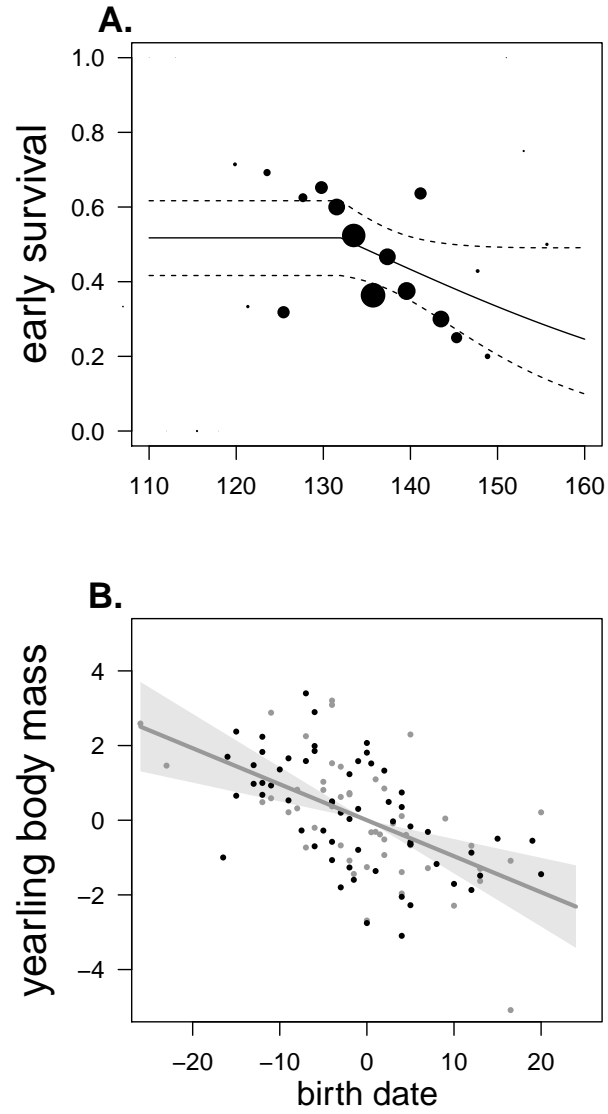


Fig. 1

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Fig. 2

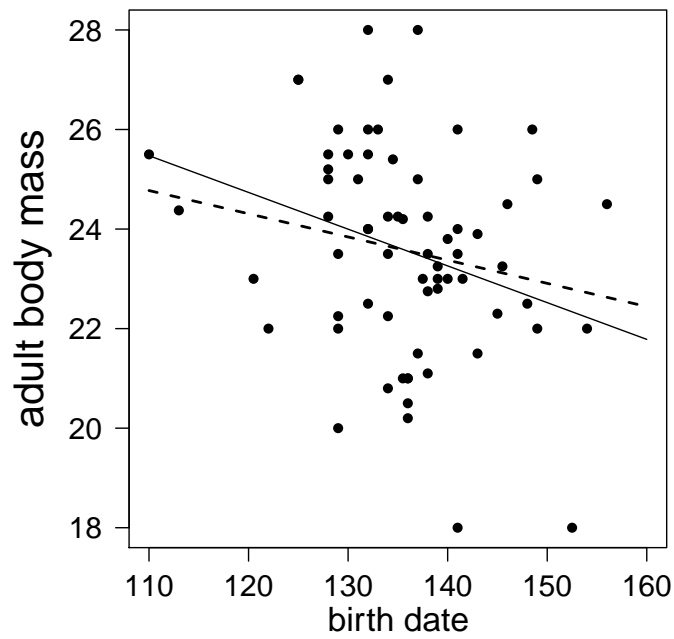


Fig. 3

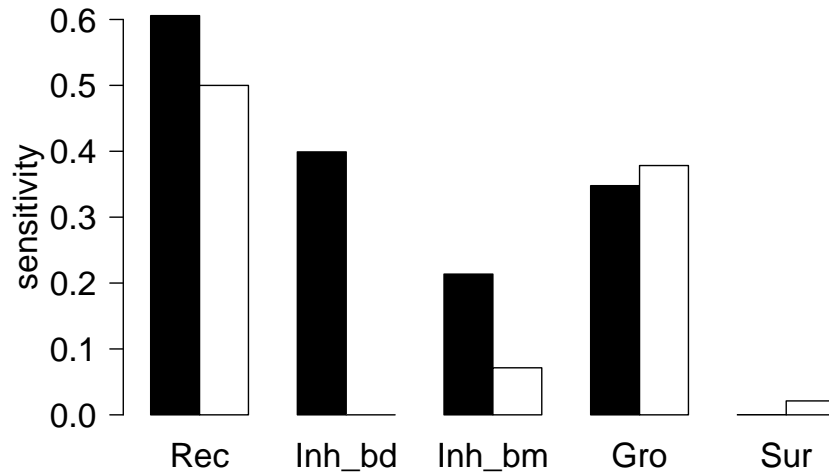
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Fig. 4

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