

Disentangling direct and growth-mediated influences on early survival: a mechanistic approach

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Summary

1. Early survival is a key life-history trait that often accounts for a large part of the variation in individual fitness and shapes population dynamics. The factors influencing early survival are multiple in large herbivores, including malnutrition, predation, cohort variation or maternal effects. However, the mechanistic pathways connecting these drivers to variation in early survival are much less studied. Indeed, whether these factors influence early survival directly or indirectly through early growth remains to be disentangled.

2. In this study, we used a path analysis to separate the direct and indirect (i.e. mediated by early growth) pathways through which sex, birth date, cohort and family effects influence early survival. We used a large data set of marked roe deer newborns collected from 1985 to 2010 in the intensively monitored population of Trois Fontaines (France).

3. We found that most drivers have indirect influences on early survival through early growth. Indeed, cohort effects influenced early survival through the indirect effect of precipitation around birth on early growth. Precipitation also had direct effects on early survival. Family effects indirectly influenced early survival. Twins from the same litter grew at about the same rate, so they had the same fate. Moreover, some factors, such as birth date, had both direct and indirect effects on roe deer early survival, with fawns born early in the season benefiting from high early survival both because they have more time to grow before the harsh season and because they grow faster during their first days of life than late-born fawns.

4. These findings suggest that most drivers of early survival previously identified in large mammalian herbivores may affect early survival primarily through their influence on early growth. Disentangling the direct and indirect pathways by which different factors influence early survival is of crucial importance to understand the mechanisms shaping this key component of individual fitness.

Key-words: birth mass, early growth, maternal effect, path analysis, population density

Introduction

Juvenile survival has been designed as a key life-history trait shaping life-history strategies (Stearns 1992). For instance, when juvenile survival is lower than adult survival, iteroparity should be selected for (Charnov & Schaffer 1973). Adult survival is high with relatively low variability in time in populations of long-lived species of

large herbivores, whereas juvenile survival varies substantially and often drives observed variation in population growth rate (Gaillard *et al.* 1998; Gaillard *et al.* 2000). Moreover, variation in juvenile survival often accounts for a large part of the observed variance in fitness measurements such as lifetime reproductive success in long-lived iteroparous species (Clutton-Brock 1988; Newton 1989). Identifying the factors shaping variation in juvenile survival and quantifying their relative influence is thus of crucial importance to understand the evolution of life-history strategies.

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In temperate ecosystems, juvenile survival can be split between summer (i.e. survival from birth to the onset of winter, which corresponds to early survival) and winter (from the onset of winter to recruitment) survival (Clutton-Brock, Guinness & Albon 1982). While winter survival is largely determined by body mass reached at the onset of winter and by winter severity, a large number of factors have been reported to influence early survival in large herbivores, including density and climate at the population level, and phenotypic attributes at the individual level (see Gaillard *et al.* 2000, for a review). In particular, birth mass and early growth strongly affect early survival both within and among years (Clutton-Brock *et al.* 1992; Gaillard *et al.* 1997; Jones *et al.* 2005). For instance, early mortality has been related to food resource limitation in reindeer (*Rangifer tarandus*, Tveraa *et al.* 2003) and roe deer (*Capreolus capreolus*, Andersen & Linnell 1998). Indeed, underfed neonates can have an increased sensitivity to disease when immunity transfer from mother to neonate has failed partially (Sams *et al.* 1996) or when they cannot escape predators. Early growth is thus expected to be a crucial trait through which maternal, environmental and individual factors (described below) can influence early survival. As a consequence, it is difficult to disentangle the mechanistic pathways (direct vs. indirect through early growth) connecting these factors to early survival.

Maternal effects (Mousseau & Fox 1998; Keech *et al.* 2000; Jones *et al.* 2005) account for a large part of observed variation in early survival. In large mammals, heavier and more experienced females consistently have higher reproductive success than light and/or young females (Georges & Guinet 2000). Experienced and high-quality females give birth to heavy neonates (Birgersson & Ekvall 1997) that will benefit from a high early survival (Albon, Clutton-Brock & Guinness 1987). The quality of the fawn habitat, which has the main influence on early survival and individual fitness (Pettorelli *et al.* 2003; McLoughlin *et al.* 2007), is also transmitted by the mother to its offspring.

Among environmental effects, predation is one of the main causes of early mortality in large herbivores (Bertram & Vivion 2002; Jarnemo *et al.* 2004). High population density or harsh weather conditions decrease early survival (Douglas & Leslie 1986; Clutton-Brock *et al.* 1992). Nonetheless, all environmental variables that affect resource availability often indirectly influence early survival (Pettorelli *et al.* 2005) through a reduction in offspring early growth. Clutton-Brock *et al.* (1992) showed that population density negatively affected birth mass; one-third of the total indirect effect of density on early survival in Soay sheep was accounted for by birth mass.

At the individual level, variation in early survival is induced by among-individual differences in genetic factors, birth date and/or sex (Pemberton *et al.* 1988; Jones *et al.* 2005) in addition to early growth. Birth date can influence early survival through predation because neonates born during the peak of births often have a lower probability of being preyed upon than

individuals born earlier or later in the season (Ims 1990; Gregg *et al.* 2001). On the other hand, the synchrony between birth date and resource availability (Rutberg 1987) can also indirectly affect early survival through early growth. Similarly, sex can affect simultaneously both early survival and early growth, but with possible opposite effects (Kraus *et al.* 2013). In species with high intensity of sexual selection, males are expected to have higher early growth than females. Because of their greater allocation to body growth, males are more susceptible to food shortage and suffer from a higher early mortality than females when resources are scarce (Clutton-Brock, Albon & Guinness 1985; Bonenfant *et al.* 2009). Moreover, adult females have a higher probability of survival than males in most polygynous and dimorphic mammals (Promislow 1992), and sex differences can also occur in early survival (Clutton-Brock, Albon & Guinness 1985).

In this study, we aimed first to identify the factors shaping early survival, then to assess the pathways by which these factors influence early survival and lastly to quantify the relative contribution of these factors in driving observed changes in early survival, in a polytocus large herbivore, the roe deer. We studied a population with highly variable early survival among years (ranging between 0.3 and 0.9). To understand how cohort variation, individual characteristics (birth date and sex) and maternal effects shaped early survival, we used a path analysis to separate the direct and indirect effects (through early growth) of these factors. More specifically, we tested the following predictions: (i) because of the weak predation by large carnivores in our study site and because direct mortality due to extreme environmental conditions is rare in large herbivores (Gaillard *et al.* 2000; Garel *et al.* 2004), we expected that cohort effects should influence early survival through an indirect effect mediated by early growth. (ii) In our roe deer population, birth date influences early survival (Plard *et al.* 2014a) probably because early-born individuals have access to higher quality resources than late-born ones. As predicted from the link between early growth and resource availability (Rutberg 1987), we expect that early-born fawns should more greatly benefit from higher early growth than late-born fawns. This leads to a mostly indirect effect, mediated by early growth, of birth date on early survival. (iii) Because maternal effects arise mostly by variation in milk production in mammals, we expected that the influence of maternal effects on early survival should be mainly driven by early growth.

Materials and methods

STUDY AREA AND POPULATION

The roe deer population of Trois Fontaines is located in an enclosed forest of 1360 ha in the Haute-Marne (48°43'N, 2°61'E, north-eastern France). The forest is highly productive (Pettorelli

et al. 2006), mainly composed of oak (*Quercus* sp.) and beech (*Fagus sylvatica*). Hornbeam (*Carpinus betulus*) and brambles (*Rubus* sp.), which occur in the understorey, constitute the main food resources of roe deer. Roe deer take advantage of a continental climate with mild springs. This population has been intensively monitored since 1975 by the Office National de la Chasse et de la Faune Sauvage (Gaillard *et al.* 1993a). Each year, between 8 and 12 days of drive-netting capture [a method approved by the French Ministry of Environment (articles L.424-1, R.411-14 and R.422-87 of the French code of environment)] are organized from mid-December to mid-March. Between 100 and 250 people drive roe deer into nets. About one half of the roe deer population is captured every year. All captured individuals (120–300 by year) are sexed and weighed to the nearest 100 g, marked and then released in the forest plot where they were captured.

BIRTH DATE AND BODY MASS

The birth season lasts from mid-April to mid-June and more than 90% of the births occur in May (median: May 16th that is constant over years, Gaillard *et al.* 1993a; Plard *et al.* 2013). From 2 years of age onwards, female roe deer give birth each year to one or two fawns. Each year from 1985 to 2010, systematic searches for fawns began in mid-April and 21 to 63 fawns were captured per year. Fawn manipulation lasted <15 min. Experienced people handled, sexed and weighed the fawns. Starting from the location of a fawn, rotated searches were conducted in circles of increasing size up to a diameter of approximately 150 m to find a potential twin. Age was estimated by inspection of umbilicus characteristics and behaviour at marking (Jullien, Delorme & Gaillard 1992). Birth date was then back-calculated based on estimated age and date of capture. Error on age estimation was less than about 2 days (Gaillard *et al.* 1993a). All fawns older than 20 days were removed from the analysis because error on age estimation increases with the age of the fawn.

EARLY SURVIVAL

We defined early survival as the survival of neonates from birth to 8 months of age, when annual net captures took place (from December to March). We used data on individuals born between 1985 and 2010. Each animal has been captured on average every 2 years (Gaillard *et al.* 2003). We excluded the last 4 years (2011–2014) to have accurate assessment of survival based on winter captures (see Pettorelli *et al.* 2005, for further details).

ENVIRONMENTAL DRIVERS

Annual daily temperatures and precipitation were recorded by a Météo France weather station located at Saint-Dizier (<5 km from the study area). Annual adult roe deer density was estimated using a generalization of the Cormack–Jolly–Seber capture–recapture model (Gaillard *et al.* 2003). The high proportion of individually marked deer (70%) during most years gave reliable population density estimates. Weather conditions during the birth season as well as density influence early survival and early growth in roe deer (Gaillard *et al.* 1997; Andersen & Linnell 1998). Consequently, we tested for the direct and indirect influences of density, mean temperature around birth time (average of the daily temperatures from 15 days before to 15 days after the median birth date) and sum of precipitation around

birth time (measured on the same period as temperature around birth time) on early survival. This period covers more than 90% of fawn births.

STATISTICAL ANALYSIS

First, we investigated the direct effect of early growth and the direct and indirect (mediated by early growth) influences of cohort, birth date, sex and age on early survival, using a path analysis (Shipley 2002) in a Bayesian framework using the package RJAGS (using jags) in R (Plummer & Stukalov 2014):

- *Early growth*: As fawn body mass increases with age during early life, we investigated the influence of early growth rather than fawn body mass at capture on early survival. We calculated the residuals of a generalized additive model linking fawn body mass to age at capture to estimate early growth. Early growth is therefore a measure of fawn body mass corrected for age (a compound of birth mass and early growth rate). All other tested indirect effects were added to this generalized additive model as linear predictors (see Supporting information, Appendix S2 for a description of the model).
- *Cohort*: We included the year of birth of fawns in the model as a fixed factor with 26 levels. We did not include year as a random factor because the quality of the cohort did not follow a normal distribution and good and poor cohorts were more frequent than average cohorts. Fitting a fixed cohort effect allowed us to include differences of quality among years (caused by any potential environmental factors, e.g. temperatures, precipitation, availability of resources) that influence early survival either directly or indirectly (through early growth).
- *Birth date*: Birth date can directly influence early survival. For a given growth rate, fawns born earlier benefit from a longer time to reach a threshold mass beyond which thermoregulation is no longer an issue. Moreover, birth date can influence early survival indirectly through early growth because birth date closely matches the availability of high-quality food. The peak of high-quality food often occurs before the first roe deer births, and this peak has recently advanced; however, roe deer birth season has not changed (Plard *et al.* 2014a). This leads to the expectation that a fawn born early in the season will have a higher early growth than a fawn born late in the season. Moreover, we have previously shown that early survival is linked to birth date through a threshold relationship (with constant survival until the 12th of May, followed by decreasing survival, Plard *et al.* 2014a). We thus modelled the direct effects of birth date on early survival with a threshold model and its indirect effects through early growth with a linear effect because we did not expect a threshold effect of birth date on early growth. We did not test for a quadratic effect of birth date because there is a strong selective pressure for being born very early in the season in roe deer since the earliest born fawns have the highest early survival (Plard *et al.* 2014a).
- *Sex*: Although we previously found that females and males have similar early survival patterns (Gaillard *et al.* 1997), males are about 1 kg heavier than females at the onset of their first winter (Gaillard *et al.* 1996). We thus tested for both direct and indirect effects of sex on early survival in our updated and larger data set.

- *Age*: A fawn captured at 20 days of age should have higher early survival than a fawn captured at 1 day of age for two reasons. First, the highest fawn mortality occurs in the first days of life in roe deer and other ungulates in temperate ecosystems. Secondly, viability selection on fawns should lead to an increasing average viability of fawns as they grow older because frail individuals generally die sooner than more robust individuals. We thus included a direct effect of age on early survival and tested both for linear and quadratic influences (to test for a nonlinear relationship between age and early survival). In order to correct for the age of capture, we also included an effect of age at capture on fawn body mass in the part of the model used to estimate early growth (see description of the variable early growth).

The most complex model included a direct effect of early growth on early survival and both direct and indirect effects of age, cohort, birth date and sex on early survival. We modelled early survival with a binomial distribution and a logit link and fawn body mass using a Gaussian distribution ($n = 1036$ fawns). To minimize the number of models to fit, we sequentially simplified the most complex model, removing direct and indirect effects of the different variables (cohort, age, sex, birth date and early growth in this order) except for the indirect effect of age that was included in all models (to estimate early growth). We selected the best model (M0) using the deviance information criterion (DIC, Spiegelhalter *et al.* 2014). Each variable, including early growth, was standardized in order to compare the effect size of the different variables by subtracting the mean of all variables and dividing by two standard deviations (only for continuous variables, see Gelman 2008).

Secondly, to identify which environmental variables could account for the effect of cohort, we replaced the 26-level factor cohort variable with a two-way interaction between density and temperature, and between density and precipitation. We included year as a continuous variable in these models to correct for the decreasing trend in early survival previously reported in the studied population (Plard *et al.* 2014a). Because 1985 was characterized by a particular combination of high density and precipitation, we removed this year from the data set in this analysis ($n = 989$ fawns) in order to avoid the selection of environmental variable due only to this particular year. DIC was used to select the best model of early survival including environmental drivers. Whether direct or indirect effects of cohort were retained or not in the M0 model, we consistently included direct and indirect effects of these continuous environmental drivers on early survival. Indeed, the large number of parameters required to fit the cohort effect could prevent its selection by DIC in the model M0, despite a detectable influence of environmental drivers (Lebréton, Choquet & Gimenez 2012). We estimated the proportion of deviance explained by each environmental variable using an analysis of deviance (ANODEV; Skalski, Hoffman & Smith 1993).

Thirdly, we investigated the direct and indirect influences of family (i.e. fawns from the same litter) on early survival using a restricted data set including only twins ($n = 263$ pairs of twins). We thus fitted the M0 model to the restricted data set and analysed the direct and indirect effects of family on early survival using DIC. We included family as a random effect on the intercept of both relationships explaining early survival [$u \sim n(0, \sigma_u^2)$] and fawn body mass [$v \sim n(0, \sigma_v^2)$].

We performed Bayesian analyses providing non-informative prior distributions with normal distribution of mean 0 and vari-

ance 10^3 for regression slopes, and a uniform distribution over the interval $[0, 100]$ for standard deviation of early growth residuals and standard deviations of random effects. We generated three chains of length 11 000 and used the first 1000 as burn-in for our first and second analyses. For the third analysis on family effects, we generated three chains of length 51 000 and used the first 1000 as burn-in. The fit of the models to the data was evaluated through inspection of the normality of the residuals of early growth and through graphical inspection of residuals of early growth and of the binned residuals of early survival. We also performed posterior predictive checks (Gelman & Hill 2007) to evaluate the fit of the model to the data (see Supporting information, Appendix S1, Figs S4 and S5). We conducted a prior sensitivity analysis to investigate how the prior distribution influences the model selection using a normal distribution with variance of 1 and 10^6 and a uniform distribution on the interval $[0, 1]$ and $[0, 1000]$ (see Supporting information, Tables S1 and S2). The proportion of variance in early survival and fawn body mass accounted for by a specific model was estimated using R^2 by subtracting 1 from the variance of the residuals of the model over the variance of the variable of interest, following the technique described in Gelman & Pardoe (2006; see Supporting information, R script in Appendix S2).

Results

EARLY GROWTH

Fawn body mass showed two phases of growth (Fig. 1). Neonates grew linearly at a rate of about 283 g per day until 4 days of age. Beyond 7 days, fawns grew by about 120 g per day until 15 days of age. Birth mass was estimated at 1.593 kg. In the following analyses, early growth corresponds to the residuals of the generalized additive model between fawn body mass and age.

DIRECT AND INDIRECT EFFECTS OF BIRTH DATE, SEX AND COHORT ON EARLY SURVIVAL

To select the best model describing early survival, we first successively simplified a model including the effects of cohort, sex, age (with a quadratic effect), birth date and early growth on early survival ($n = 1036$ fawns, Table 1). Only birth date, age (as a linear effect) and early growth had a direct effect on early survival. We found indirect effects of sex and cohort on early survival through early growth. In addition to its direct effect on early survival, birth date also negatively influenced early survival through early growth (removing any of these variables from the best model led to $\Delta\text{DIC} > 2$, Table 1). This model (Fig. 2) accounted for 9 and 76% of the observed variation in early survival and fawn body mass, respectively. Age, early growth and birth date accounted for 42, 39 and 19%, respectively, of the explained variation in early survival. Age, cohort, birth date and sex accounted for 92, 7.5, 0.25 and 0.25%, respectively, of the explained variation in fawn body mass.

Early survival increased linearly with age, which showed the strongest effect [slope on the logit scale for

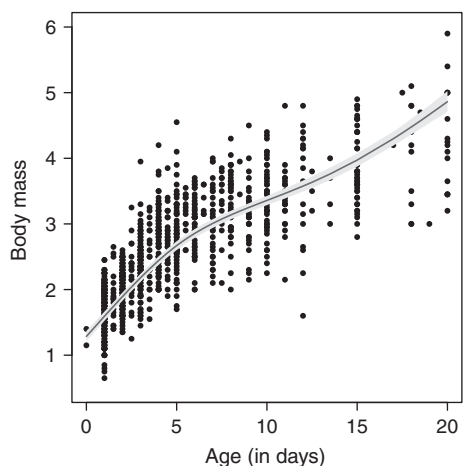


Fig. 1. Early growth of roe deer fawns in the population of Trois Fontaines, France. Early growth was measured as the residuals of the relationship between body mass and age at capture.

the standardized variable: 1.026 [0.750, 1.312] (here and thereafter, 95% credible intervals are presented in square brackets, Fig. 2). A 1-day-old fawn on average had a probability of survival (0.31) two times lower than a 15-day-old fawn (0.69). After birth, each additional day of life increased the chance of surviving to 8 months of age by 9% (odd ratio). Early growth positively influenced early survival (Fig. 3b, slope on the logit scale: 0.805 [0.535, 1.081]). Moreover, early growth mediated many indirect effects on early survival. In accordance with our first prediction (i), indirect effects of cohort on early survival were mediated by early growth. In agreement with our second prediction (ii), birth date also indirectly influenced early survival through a negative relationship with early growth (Fig. 3a). Nevertheless, birth date had a main threshold direct effect on early survival (Fig. 3a) with fawns born late in the birth period (30th May) having a lower probability of survival (0.28) than fawns born before

May 12th (0.47). Sex had a small indirect effect on early survival through early growth (slope: -0.033 [$-0.064, -0.003$] compared to -0.051 [$-0.082, -0.020$] for the indirect effect of birth date on early survival through early growth), with females exhibiting slightly lower early growth than males (Fig. S1, Supporting information). It is important to note that the parameter estimates reported above are similar between alternative models with similar DIC scores (Table S3, Supporting information).

ENVIRONMENTAL VARIABLES

We investigated the influence of cohort variation on early growth and early survival by replacing the cohort (modelled as a factor with 26 levels) with the following continuous environmental variables: year, density, mean temperature around birth and sum of precipitation around birth (Table 2, Fig. S2, Supporting information). The best model included the direct and indirect effects of year and precipitation around birth on early survival, and the indirect effect of density on early survival through early growth. The indirect effect of precipitation (0.069 [0.032, 0.105]) was more important than the indirect effects of birth date (-0.048 [$-0.080, -0.016$]) and sex (-0.033 [$-0.066, -0.001$]; Fig. S2, Supporting information). However, the direct effect of precipitation (0.406 [0.085, 0.728]) was less important than the direct effects of birth date (-0.661 [$-0.944, -0.381$]) and early growth (0.837 [0.552, 1.134]). As a result, early survival could increase by 46% between years of low and high precipitation (Fig. 4, compared to an increase of 68% between late- and early-born fawns). The indirect effect of density was weak (slope: 0.043 [0.015, 0.072]) with a 4.5% increase in early survival between years of very low and very high densities (Fig. 5). The model including continuous environmental variables accounted for 11 and 74% of the total variation in early survival and

Table 1. Selection of models describing the direct and indirect [through early growth (EGrowth)] effects of sex, cohort, birth date (BDate), age at capture and early growth on early survival of roe deer fawns. Dev is the deviance of the model, Pd is the estimated number of parameters, and Δ DIC indicates the difference in the deviance information criterion between two competing models. The selected model is in bold

	Direct effect: Early survival \sim	Indirect effect: EGrowth \sim	Dev	Pd	Δ DIC
1	EGrowth + age + age ² + Bdate + sex + cohort	Bdate + sex + cohort	1289	63	7
2	EGrowth + age + age ² + Bdate + sex + cohort	Bdate + sex	1510	37	202
3	EGrowth + age + age ² + Bdate + sex	Bdate + sex + cohort	1308	38	0
4	EGrowth + age + age ² + Bdate + sex	Bdate + sex	1529	13	196
5	EGrowth + age + Bdate + sex	Bdate + sex + cohort	1308	36	0
6	EGrowth + Bdate + sex	Bdate + sex + cohort	1363	36	54
7	EGrowth + age + Bdate + sex	Bdate + cohort	1312	35	3
8	EGrowth + age + Bdate	Bdate + sex + cohort	1309	36	0
9	EGrowth + age + Bdate	Bdate + cohort	1312	35	2
10	EGrowth + age + Bdate	Sex + cohort	1318	35	8
11	EGrowth + age	Bdate + sex + cohort	1325	35	15
12	EGrowth + age	Sex + cohort	1334	34	23
13	Age + Bdate	Bdate + sex + cohort	1341	35	31

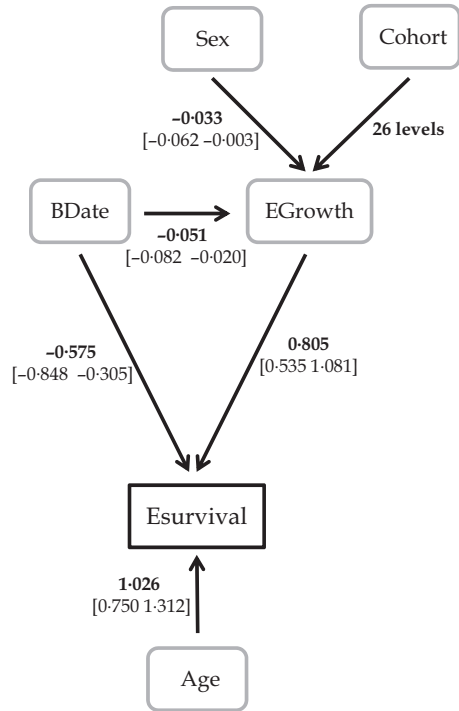


Fig. 2. Path analysis showing the direct and indirect influences of early growth (EGrowth), birth date (BDate), sex, age at capture and cohort on early survival (ESurvival) in the population of roe deer at Trois Fontaines, France.

fawn body mass, respectively (compared to 9 and 77% for the model including a cohort effect and 9 and 73% for a model without any cohort or environmental effect). Precipitation around birth and density accounted for 12 and 8% (ANODEV) of the average variation among cohorts in early survival, respectively.

FAMILY EFFECTS

To look at the influence of family effects on early survival, we used a restricted data set including only twins ($n = 263$ pairs). We fit the best model which included a cohort effect (M0 selected in Table 1) to this restricted data set and analysed direct and indirect effects of family. Effect sizes were similar in models fitted to the whole or the restricted data set (Fig. 2 and Fig. S3, Supporting information). In accordance with prediction (iii), indirect family effects on early survival through early growth were strongly supported by our model ($\sigma = 0.195$ [0.171, 0.221], $\Delta DIC = 274$ without the indirect family effect, Fig. S3, Supporting information). These results show that fawns from the same pair often share the same early growth and thereby the same fate. Adding a direct effect of family to this model weakly decreased the DIC ($\Delta DIC = -4$, for the direct effect of family: $\sigma = 0.669$ [0.136, 1.217]). However, the number of parameters was underestimated (262) in this model compared to the one with only an indirect effect (215). Thus, the direct effect of

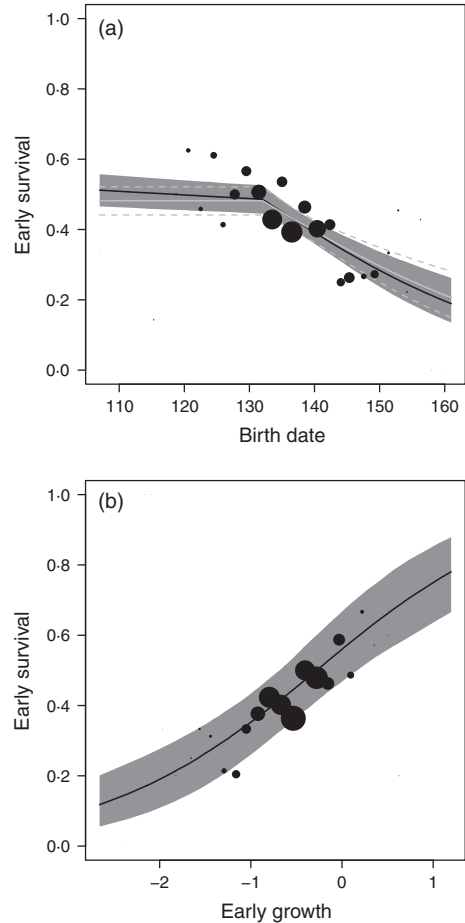


Fig. 3. Influences of birth date and early growth on early survival of roe deer fawns in the population of Trois Fontaines, France (95% confidence intervals are presented). (a) Direct and indirect (through early growth) influences of birth date on early survival. Dotted grey lines represent the direct effect only of birth date on early survival. (b) Influence of early growth on early survival.

family was only weakly supported by our model. The model including direct and indirect family effects accounted for 15 and 90% of the total variation in early survival and fawn body mass, respectively (compared to 7 and 76% for the best model without a family effect fitted to the restricted data set).

Discussion

We found that most factors shaping the variation in early survival of roe deer have indirect effects through early growth (Table 3). Most previous studies have suggested that the factors shaping variation in early survival only have direct effects and these studies did not investigate the possibility of indirect effects (Gaillard *et al.* 1997; Jones *et al.* 2005). By accounting for indirect effects, our study shows that the effect of early growth on early survival mediates the influence of family, environmental or individual effects on early survival.

Table 2. Selection of models describing the direct and indirect [through early growth (EGrowth)] effects of population density (den), mean temperature around birth (BTemp) and sum of precipitation around birth (BPrec) on early survival (ESurv). All models included a direct effect of early growth, age and birth date and an indirect effect of birth date and sex (through early growth) on early survival of roe deer fawns. (a) The indirect effects on early survival were first tested. (b) Then, the direct influences of environmental drivers on early survival were investigated using a model including all the variables selected in (a). Dev is the deviance of the model, Pd is the estimated number of parameters, and Δ DIC indicates the difference in the deviance information criterion between two competing models. The selected model is in bold

	Dev	Pd	Δ DIC
(a) Indirect effect: $EGrowth \sim Bdate + sex + year+$			
den*BPrec + den*BTemp	1314	23	10
den*BTemp + BTemp	1314	22	9
BPrec + den*BTemp	1315	22	10
den*BPrec	1313	21	7
den*BTemp	1327	21	21
den + BPrec + BTemp	1314	21	8
den + BPrec	1313	20	6
den + BTemp	1327	20	19
BPrec + BTemp	1323	20	15
den	1326	19	17
BTemp	1333	19	25
BPrec	1322	19	13
1	1332	18	23
(b) Direct effect: $ESurv \sim EGrowth + age + Bdate + year+$			
den*BPrec + den*BTemp	1313	20	6
den*BPrec + BTemp	1312	18	4
BPrec + den*BTemp	1312	19	4
den*BPrec	1312	18	2
den*BTemp	1317	18	7
den + BPrec + BTemp	1311	18	2
den + BPrec	1311	16	0
den + BTemp	1316	17	5
BPrec + BTemp	1313	17	2
den	1315	15	3
BTemp	1318	15	6
BPrec	1312	15	0
1	1317	15	5

In populations subjected to weak predation pressure, early survival of offspring depends on early growth. Deer fawns with high early growth display a higher probability of survival until maturity, as commonly found in many vertebrates (Albon, Clutton-Brock & Guinness 1987; Magrath 1991). High early growth should favour efficient thermoregulation and immunity against diseases (Sams *et al.* 1996). Moreover, larger fawns can move easily and farther away to find sheltered habitats that will enhance high early survival (Van Moorter *et al.* 2009). We found that fawns exhibited a linear growth of 120 g per day between 5 and 20 days of age, close to what has been previously reported (135–145 g in roe deer during the first month, Gaillard, Delorme & Jullien 1993b; Portier *et al.* 2000). However, we found evidence for an accelerated early growth of 283 g per day between 1 and 4 days of

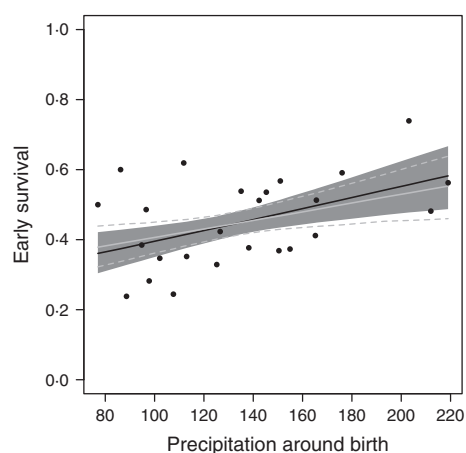


Fig. 4. Direct and indirect (through early growth) influences of the sum of birth precipitation on mean early survival of roe deer fawns in the population of Trois Fontaines, France. Dotted grey lines represent the direct effect only of precipitation on early survival.

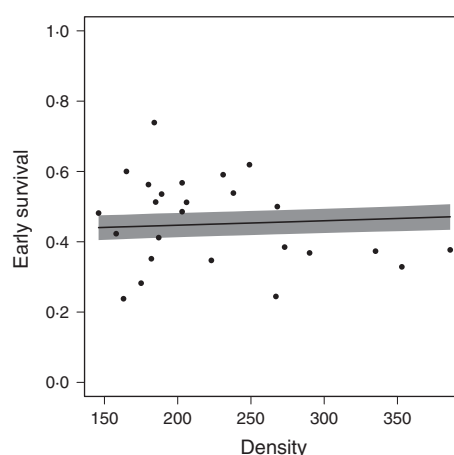


Fig. 5. Influence of density on early survival of roe deer fawns in the population of Trois Fontaines, France.

Table 3. Summary of the direct and indirect effects through early growth of birth date, cohort, sex and family on early survival on roe deer fawns at Trois Fontaines, France

Effect	Direct	Indirect
Birth date	++	+
Cohort	+	++
Sex		+++
Family	+	++

age. The existence of stages with different intensity of growth has already been proposed in black-tailed deer (*Odocoileus hemionus*) for which Cowan & Wood (1955) identified two phases: one until 7 days and a second from 7 to 21 days when early growth decreases by one half on average. Moreover, the metabolic rate of roe deer fawns increases during the first 7 days, which could be related to the development of thermoregulation (Weiner 1977).

Early survival also increased directly with age. Most deaths occur in the first weeks of life in large herbivores (Gaillard *et al.* 2000) and often in the very first days of life, which supports a strong link between early growth and early survival.

Early growth mediated family effects on early survival. Sibling neonates shared similar fate in roe deer, especially in poor conditions (Gaillard *et al.* 1998). Such family effects have been reported in other polytocous vertebrates such as cheetah (*Acinonyx jubatus*, Pettorelli & Durant 2007) or common lizard (*Lacerta vivipara*, Massot & Clobert 2000). Our study reveals that this occurs in roe deer because sibling fawns share a similar growth trajectory. Maternal phenotypic attributes are expected to account for most indirect family effects. High-quality mothers (*sensu* Wilson & Nussey 2010; Plard *et al.* 2014b; in the case of roe deer) often give birth earlier and provide more prenatal care, giving birth to two heavy newborn in roe deer (Andersen *et al.* 2000) and other polytocous ungulates (Jones *et al.* 2005). Family effects in early growth have also been suggested in pronghorn (*Antilocapra americana*), another polytocous species of large herbivore (Byers & Hogg 1995). In roe deer, family effects are most pronounced in poor cohorts (Gaillard *et al.* 1998) when fawn survival depends on mother habitat quality (Pettorelli *et al.* 2005). In harsh environmental conditions, when females are unlikely to raise twins, most females allocate energy to their own survival and jeopardize the survival of both of their fawns, sometimes actively abandoning them. Raising a single fawn successfully requires more than half of the energy needed to successfully raise twins (Oftedal 1984; Andersen & Linnell 1997). We thus suggest that the high variability in early survival reported for polytocous species (Gaillard *et al.* 2000 for a review in large herbivores) could be due to this all vs. nothing allocation of energy to current reproduction depending on the quality of environmental conditions.

Environmental effects on early survival are common in large herbivores (Clutton-Brock *et al.* 1987; Clutton-Brock *et al.* 1992) and revealed by our study to be mostly indirect in roe deer. Indeed, cohort effects markedly influence early growth through variation in the amount of high-quality resources available during late gestation and early lactation. Females benefit from abundant precipitation in May, when they can selectively choose the highest quality resources. Precipitation around birth also directly influenced early survival, probably preventing the occurrence of droughts, which can be fatal to young fawns. This study suggests that cohort effects mainly influence early survival through growth from birth to maturity. The positive effect of density on fawn body mass (Fig. 5) remains very weak and was not previously reported in this population (Gaillard *et al.* 1997). This effect could be generated by environmental effects correlated to density that would induce some heterogeneity in female quality among years and thus in the early survival of their fawns.

Birth date has both direct and indirect effects on early survival in roe deer, and we expect this is the case in most large herbivores in temperate ecosystems. Direct effects of birth date on early survival must be mediated by the time window an individual can grow before the onset of the harsh season (Feder *et al.* 2008). Indirect effects of birth date on roe deer early survival through early growth occur because fawns born early in the season have access to higher quality milk (Plard *et al.* 2014a), while late-born fawns have access to poorer quality milk. Early-born fawns benefit from a higher early growth, which allows them to avoid thermoregulation issues and the risk of abandonment by their mother if the quantity of available resources decreases. Among the other individual differences that influence early survival, we found that sex had a weak and indirect effect on early survival. Females had a lower early growth than males. This weak sex difference [difference of early growth of 0.068 and 0.071 g per day between males and females in Gaillard *et al.* (1993b) and the present study, respectively] was not statistically significant in previous studies on this slightly size dimorphic and polygynous species, probably due to a lack of power (Gaillard *et al.* 1993b; Andersen & Linnell 1997; Portier *et al.* 2000).

In conclusion, multiple factors that shape observed variation in early survival predominately influence it through early growth. The strong link between early survival and early growth demonstrates that the high variability in early survival in iteroparous species is directly linked to a high variability in neonate early growth and birth mass and thereby to the quality of environmental conditions. In polytocous and iteroparous species, females facing harsh environmental conditions are unlikely to raise any fawn if they follow this all vs. nothing strategy. However, females of monotocous species, which allocate less to reproduction than polytocous species, can increase the amount of care to counteract adverse environmental effects by allocating more energy to their young, thereby improving the early survival of their offspring while avoiding the jeopardization of their own survivorship. In roe deer, even if some females of higher quality perform better than others by giving birth earlier (Plard *et al.* 2014b) and allocating more energy to their fawns, the main cause of variation in early survival is environmental conditions. This is in concordance with the roe deer life-history strategy which has evolved in unpredictable environments. Roe deer mothers should have highest success in investing in reproduction at the same level each year and then adjusting their allocation according to available resources.

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Data accessibility

The data are included in the Table S4 of the Supporting information.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Figure S1. Influence of sex on early growth of roe deer fawns in the population of Trois Fontaines, France.

Figure S2. Path analysis showing the direct and indirect influences of early growth, birth date, sex, age at capture and environmental drivers on early survival (model selected in Tables 1 and 2) in the population of roe deer at Trois Fontaines, France.

Figure S3. Path analysis showing the indirect influence of family effects in addition to the variables selected in Table 1 on early survival in the population of roe deer at Trois Fontaines, France.

Figure S4. Posterior predictive checks of the model M0, presented in Fig. 2 including cohort as a factor.

Figure S5. Posterior predictive checks of the model presented in Fig. S2 including environmental variables as drivers (instead of cohort as a 26 level independent factor).

Table S1. Prior sensitivity analysis on the selection of models describing the direct and indirect [through early growth (EG)] effects of sex, cohort (coh), birth date (BD), age at capture (a) and early growth on early survival of roe deer fawns.

Table S2. Prior sensitivity analysis on the selection of models describing the direct and indirect [through early growth (EGrowth)] effects of population density, mean temperature around birth (BTemp) and sum of precipitation around birth (BPrec) on early survival.

Table S3. Comparison of estimated parameters and their 95% confidence interval among models of equivalent DIC (see Table 1 for the description of the models).

Table S4. Data.

Appendix S1. Posterior predictive checks.

Appendix S2. Script of the model selected after the analysis of family effects on early survival.