

Quantifying the influence of measured and unmeasured individual differences on demography

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Summary

1. Demographic rates can vary not only with measured individual characters like age, sex and mass but also with unmeasured individual variables like behaviour, genes and health.

2. Predictions from population models that include measured individual characteristics often differ from models that exclude them. Similarly, unmeasured individual differences have the potential to impact predictions from population models. However, unmeasured individual differences are rarely included in population models.

3. We construct stage- and age-structured models (where stage is mass) of a roe deer population, which are parameterized from statistical functions that either include, or ignore, unmeasured individual differences.

4. We found that mass and age structures substantially impacted model parameters describing population dynamics, as did temporal environmental variation, while unmeasured individual differences impacted parameters describing population dynamics to a much smaller extent once individual heterogeneity related to mass and age has been included in the model. We discuss how our assumptions (unmeasured individual differences only in mean trait values) could have influenced our findings and under what circumstances unmeasured individual differences could have had a larger impact on population dynamics.

5. There are two reasons explaining the relative small influence of unmeasured individual differences on population dynamics in roe deer. First, individual body mass and age both capture a large amount of individual differences in roe deer. Second, in large populations of long-lived animals, the average quality of individuals (independent of age and mass) within the population is unlikely to show substantial variation over time, unless rapid evolution is occurring. So even though a population consisting of high-quality individuals would have much higher population growth rate than a population consisting of low-quality individuals, the probability of observing a population consisting only of high-quality individuals is small.

Key-words: age structure, body mass, growth rate, individual random effect, integral projection model, roe deer, size structure

Introduction

Among- and within-individual variation can markedly influence population dynamics, particularly in mammals (Caswell 2001; Benton, Plaistow & Coulson 2006). Most

previous studies of factors generating individual variation in survival and reproduction have focused on size/mass, sex and age (Caswell 2001). Age and mass both influence population growth when survival and reproductive rates vary substantially between small and large individuals, or between those that are young, prime-aged and elderly (Eberhardt 1985; Gaillard *et al.* 2000b; Caswell 2001). Most studies have focused on these attributes because

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they are both important for population dynamics (Albon *et al.* 2000; Gaillard *et al.* 2000b; Caswell 2001) and often easy to measure. However, among the myriads of characters that are left unmeasured in most studies, some are known to influence survival and/or reproductive rates [e.g. behaviour (Reid *et al.* 2004), genes of known and unknown function (Peripato *et al.* 2002), disease state (Jolles, Cooper & Levin 2005)] and thus might be important for modelling population dynamics.

Age or stage structure can shape population dynamics when the age or mass structure of the population fluctuates in response to environmental variation caused by climatic conditions or intra- or interspecific competition (Coulson *et al.* 2001). The same logic applies to unmeasured individual differences: changes in the proportion of high-quality individuals within the population in response to variation in environmental conditions or population density will cause the distribution of unmeasured individual differences to change, which should alter population dynamics. Although unmeasured individual differences influence numerous life-history traits, little is known about their impact on population dynamics [but see Rees *et al.* (1999) on plants, Caswell (2011)]. Nonetheless, there is growing evidence that unmeasured characters have the potential to affect demography (Vindenes, Engen & Sæther, 2008; Kendall *et al.* 2011). For example, individuals differ in their survival and reproduction as a function of their susceptibility to stochastic factors (Kendall & Fox 2003), with individual stochasticity strongly shaping the distribution of individual lifetime reproductive success in birds (see Tuljapurkar, Steiner & Orzack (2009) on swans, *Cygnus olor* and Steiner, Tuljapurkar & Orzack (2010) on kittiwakes, *Rissa tridactyla*).

Individual differences in performance that cannot be easily attributed to a measured character (Lewis *et al.* 2006; Stopher *et al.* 2008; Aubry *et al.* 2009; Knape *et al.* 2011) are widely studied in ecology and evolution via the use of generalized linear mixed-effect models. The use of these models supports the existence of individual heterogeneity in reproductive traits (van de Pol & Verhulst, 2006) and survival (Cam *et al.* 2002) that can mask life-history trade-offs (van Noordwijk & de Jong 1986), including senescence (Nussey *et al.* 2008). Assumptions about unmeasured individual differences vary among studies, but they all aim to capture individual differences that are not accounted for by measured fixed effects such as age or mass. The influence of unmeasured characters (whether genetic, phenotypic, morphological or something else) on a life history is captured by models that include individual identity as a random effect. Such random effects have been used to estimate latent individual quality and have been interpreted as heterogeneity in individual frailty (Vaupel, Manton & Stallard 1979; Link, Cooch & Cam 2002), but they can also be generated by stochastic factors. For instance, individuals with the same latent quality are likely to have different fates in response to

random events and thereby display different trajectories of reproduction and/or survival (dynamic heterogeneity *sensu* Tuljapurkar, Steiner & Orzack 2009; Caswell 2011).

The influence of unmeasured individual differences on population growth can be estimated in two ways (Coulson 2012). First, one can compare predictions from population models parameterized with estimates obtained from statistical analyses that do, and do not, correct for unmeasured individual differences. Second, the magnitude of unmeasured individual differences in demographic performance can explicitly be incorporated into models (Rees *et al.* 1999; Ellner & Rees 2006; Lindberg, Sedinger & Lebreton 2013) to compare populations of high or low quality. We used both approaches to construct integral projection models (IPMs) for a population of roe deer. IPMs provide a useful tool to study the consequences of individual variation on demography (Vindenes, Engen & Sæther, 2008) because they offer a process-oriented way to study the dynamics of continuous character distributions (Easterling, Ellner & Dixon 2000; Ellner & Rees 2006). IPMs are straightforward to parameterize using generalized linear mixed-effect models (Ellner & Rees 2006; Jacquemyn, Brys & Jongejans 2010; Coulson 2012), and perturbation analyses can be used to explore how sensitive model predictions are to changes in parameter values (Caswell 1978; Rose, Rees & Grubb 2002; Coulson, Tuljapurkar & Childs 2010).

We compared the influence of age and mass, measured characters, with the additional (in models already including measured characters) influence of unmeasured random individual differences on the dynamics of a population of roe deer (Gaillard *et al.* 1998b, 2000a). Considering the influence of individual heterogeneity on demographic rates (Nussey *et al.* 2008), on demographic stochasticity and, on population dynamics (Kendall *et al.* 2011), we expect individual differences to impact population growth rate, net reproductive rate and generation time as well as demographic structure. Nevertheless, given the large amount of variation in body mass (Nussey *et al.* 2011) and age (Coulson *et al.* 2001) observed in populations of large herbivores, we expected that variation in body mass and age would impact population dynamics more than other unmeasured individual differences.

Materials and methods

STUDY POPULATION AND DATA COLLECTION

The studied population of roe deer inhabits an enclosed area of 1360 ha in the Trois Fontaines forest in north-eastern France (48°43'N, 2°61'W). Over the study period, population size was controlled to be around 250 individuals older than 1 year of age by yearly removals (Gaillard *et al.* 1993), except between 2001 and 2005 when an experimental manipulation of density was performed and population size peaked at 450 individuals. The roe deer is a long-lived and iteroparous species, with most females (>95%, Gaillard *et al.* 1998b) aged 2 years or older giving birth every year in May to either a single or twin fawns. The maximum

known age at death of females was 18 years, with a mean life span of 8.5 years. The demographic rates of roe deer are largely influenced by age (Gaillard *et al.* 1993, 1998a). Newborn fawns are characterized by a low survival and a rapid body growth, prime-aged individuals show a high and constant survival, body mass and reproductive rates, and demographic rates decrease among old individuals from 8 years of age. Reproductive patterns are also influenced by individual body mass (Hamel *et al.* 2009a). The population is not subject to systematic predation by large predators or by hunting, and the few animals killed by humans were right censored.

The roe deer population has been intensively monitored since 1975 by the Office National de la Chasse et de la Faune Sauvage (Gaillard *et al.* 1993). Most roe deer are marked with both numbered ear tags and leather collars. Each year, between 120 and 300 roe deer are caught between December and March. Individuals captured for the first time are sexed and marked, and all captured individuals are weighed to the nearest 100 g. The age and sex of all individuals considered here are accurately known because they were captured within their first year of life either as newborn (Delorme, Gaillard & Jullien 1988), or as 8 months old during winter captures when age is determined by the tooth eruption sequence (Flerov 1952). When possible, the identity of the mother of a fawn is assigned by direct observations of lactating behaviour or by the identification of an escaping female in the vicinity of the fawn.

ESTIMATION OF DEMOGRAPHIC RATES

We define a as age, t as time and z as the continuous measured character, body mass. IPMs model the dynamics of the distribution of a continuous character over time (Easterling, Ellner & Dixon 2000; Ellner & Rees 2006). IPMs include four functions (the demographic rates) that fully describe changes in the character distribution between two consecutive time steps (year). These are: (i) the association between the character and survival ($S(a, t, z)$); (ii) the association between the character and recruitment ($M(a, t, z)$); (iii) the probability of expressing a given character value at time $t+1$ given the character value at time t conditional on survival (Growth, $G(a, t, z|z)$); and iv) the probability of producing an offspring with a given character value at time $t+1$ given the parental character value at time t conditional on reproduction (Inheritance, $D(a, t, z'|z)$). Following standard terminology in IPM literature (Coulson *et al.* 2011; Coulson 2012), we defined inheritance as the part of the trait that is transmitted from mothers to offspring, whatever the mechanism of transmission. The distribution of body mass $n(a+1, t+1, z')$ in the population at time $t+1$ depends on the distribution of body mass $n(a, t, z)$ at time t and on the four functions. Then:

$$n(1, t+1, z') = \sum_a \int dz D(a, t, z'|z) M(a, t, z) n(a, t, z)$$

$$n(a+1, t+1, z') = \int dz G(a, t, z'|z) S(a, t, z) n(a, t, z), a \geq 1$$

Vital functions are integrated over a range larger than the observed body mass values. The continuous IPM can be approximated as a high-dimensional discrete matrix \mathbf{A} (see Appendix S1, Supporting information) (Easterling, Ellner & Dixon 2000).

We restricted the analyses to females because the required data for males (father-fawn affiliation in particular) were lacking. We thus modelled the distribution of female body mass only. To

parameterize IPMs, we estimated the four functions using regression models that included year as a random effect to correct for yearly variation of each demographic rate, body mass as a fixed covariate, age class as a fixed factor, and an individual random effect in models including the influence of unmeasured individual differences. Body mass is a good predictor of individual quality in roe deer (Hamel *et al.* 2009b) with statistically significant positive effects in all IPM functions (see Table S3). Both survival and reproduction of roe deer are strongly age structured. As in most species of large herbivores studied so far (Gaillard *et al.* 2000b), demographic performance of roe deer females first increases from yearling to prime-aged adults (from 2 to 8 years of age, Gaillard *et al.* 1993) and then consecutively decreases as a result of senescence between 8 and 11 years of age and a second after 11 years of age (Festa-Bianchet, Gaillard & Côté 2003). Thus, the most complex age structure included four different age classes (1, 2–7, 8–11, 12+). Unmeasured individual differences can be corrected for in statistical models using generalized linear mixed effect models with individual identity as a random effect on the overall intercept (Nussey *et al.* 2008). For instance, the estimated variance of unmeasured individual differences for recruitment represents the amount of individual differences that is unrelated to age and body mass if these are fitted as fixed effects in the expected recruitment.

The recruitment function adds new individuals to the population and, in our case, gives the number of offspring a female of a given age and body mass has weaned successfully (i.e. that survived until 8 months of age). The recruitment function was decomposed into two functions: the probability of successfully weaning at least one fawn (realized fertility, $F(a, t, z)$) and the probability of producing twins conditional on successful reproduction (twinning rate, $\phi(a, t, z)$). The parameters in the functions $F(a, t, z)$ and $\phi(a, t, z)$ were estimated using a generalized linear mixed model with a binomial error structure linking realized fertility or twinning rate to body mass, age, year (Y) and individual identity (I , when including unmeasured individual differences in the model) using the lme4 package in R. For the realized fertility function for instance,

$$F(a, t, z) = \frac{e^{\alpha_F(a,t) + \beta_F z(t) + \epsilon_{Y,F} + \epsilon_{I,F}}}{1 + e^{\alpha_F(a,t) + \beta_F z(t) + \epsilon_{Y,F} + \epsilon_{I,F}}}, \quad \epsilon_{Y,F} \sim N(0, s_{Y,F}^2), \epsilon_{I,F} \sim N(0, s_{I,F}^2)$$

where α and β are the intercept and the slope of the model and, s_Y^2 and s_I^2 are the variances of the random effect of year (Y) and individual identity (I), respectively.

Regressions were performed on 805 potential breeding events of 233 females for realized fertility (Fig. 1d) and on 588 effective breeding attempts of 212 females for twinning rate (Fig. 1e). The recruitment function was then $F(a, t, z) * (1 + \phi(a, t, z)) / 2$. We divided the recruitment by two because we used a female-based model. We then assumed a balanced sex ratio at recruitment. In the absence of between-sex differences in fawn survival in roe deer (Gaillard *et al.* 1997), this measure provides a reliable estimate of the number of daughters recruited by females.

The survival function removes individuals from the distribution through mortality by linking individual probability of surviving to body mass. The exact age of death was known for all females in the data set used to estimate the survival function. We consequently did not need to correct for the confounding effects of imperfect detection on survival estimates (Gimenez *et al.* 2008). For the survival function, random effects cannot reliably estimate heterogeneity in survival because a given individual

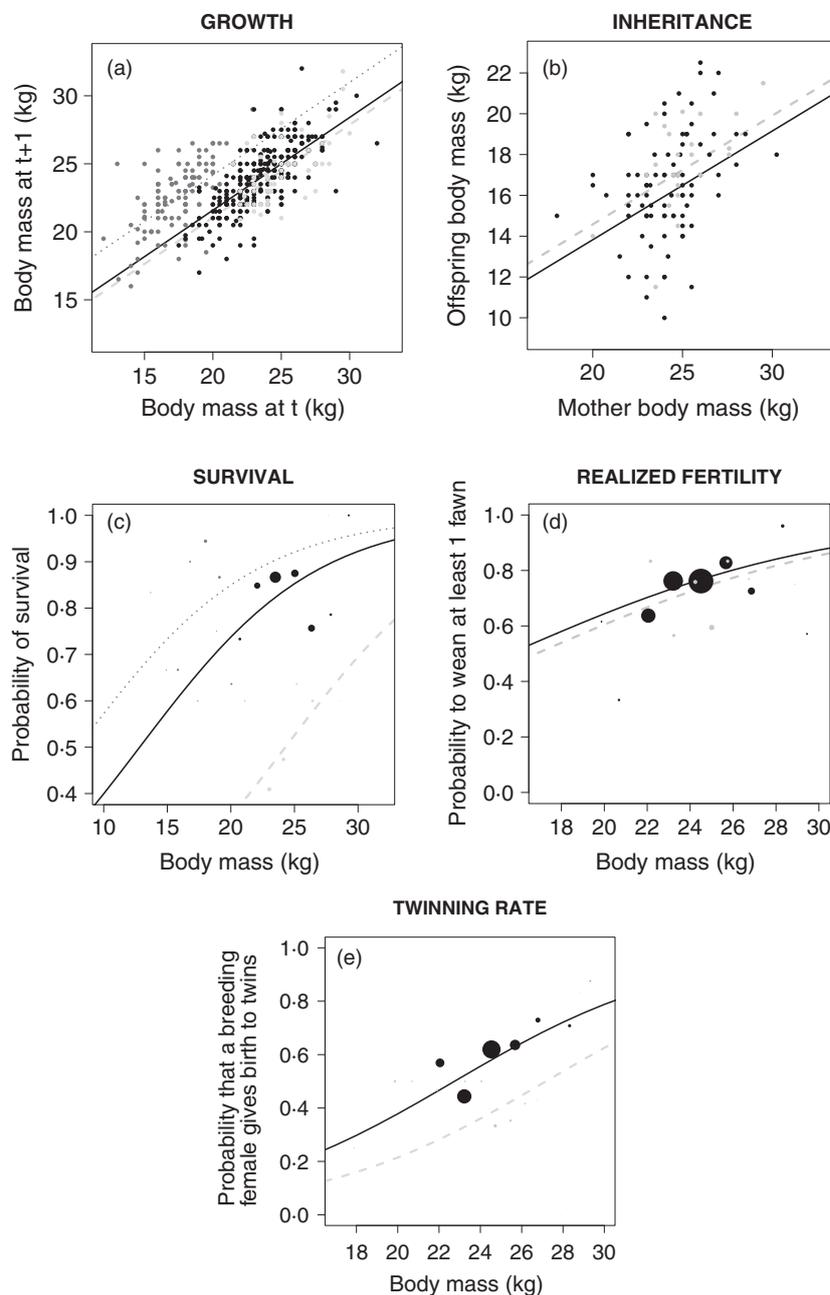


Fig. 1. Growth (a), inheritance (b), survival (c), realized fertility (d) and twinning rate (e) functions used to build the three age-class IPM (Model 6, Tables 1 and S1): yearling (dark grey dotted lines), prime-aged (2–7 years, black solid lines) and senescent (>7 years, grey dashed lines) females. For the growth (inheritance) function, at each female, body mass at t corresponds a normal distribution of female (offspring) body mass at $t+1$. The mean transitions from female body mass at t to female (offspring) body mass at $t+1$ are presented. (a,b) Each point represents an individual. (c,d) The size of points is proportional to the number of observed individual values for a given body mass.

must only die once. To assess the amount of unmeasured individual differences in the survival function, we used a frailty model. We tested for individual heterogeneity in the survival function using a parametric model with a logit link, including continuous effects of body mass and age but excluded the effect of year to minimize the number of parameters to estimate. We modelled individual frailty as a normally distributed random effect with one degree of freedom, using the functions *frailty* and *survreg* of the package ‘survival’ (Therneau 2014) in R. We found no significant effect of unmeasured individual differences on the survival function. To avoid missing any heterogeneity in frailty in the population which can have important effect on population dynamics (Vaupel & Yashin 1985), we investigated potential model convergence problems. To do so, we used a generalized linear mixed model and the package MCMCglmm to model the

survival between two time steps with a two-level (0,1) multinomial distribution and including fixed effects of body mass and age classes, and random effects of both unmeasured individual differences and year. Using this Bayesian framework, we investigated the robustness of parameter estimates with varying prior distributions and numbers of iterations. As with the frailty survival model, we found no influence of unmeasured individual differences on survival. Consequently, we used the parameters estimated from a generalized linear mixed model with both discrete age classes and continuous body mass as fixed effects, and a random effect of year to parameterize the $S(a,t,z)$ function of our IPM based on 398 episodes of survival for 99 females (Fig. 1c). The parameterization of the survival function is therefore similar to the fertility and the twinning rate functions, but excluding the individual random effect.

$$S(a, t, z) = \frac{e^{\alpha_S(a,t) + \beta_S * z(t) + \epsilon_{Y,S}}}{1 + e^{\alpha_S(a,t) + \beta_S * z(t) + \epsilon_{Y,S}}}, \quad \epsilon_{Y,S} \sim N(0, s_{Y,S}^2)$$

The growth function transforms mass within the distribution by giving the transition probability between mass at t and at $t+1$, and the inheritance function determines the mass of the new recruits in the population as a function of the mass and the age of their mother. The growth $G(a, t, z' | z)$ and inheritance $D(a, t, z' | z)$ functions were assumed to be normal probability density functions with means $\mu_{Gro}(a, t, z)$ and $\mu_{Inh}(a, t, z)$ and variances $\sigma_{Gro}^2(a, t, z)$ and $\sigma_{Inh}^2(a, t, z)$, respectively. For growth (inheritance), each body mass (maternal body mass) z at t predicts a normal distribution of body masses (offspring body mass) z' at $t+1$:

$$G(a, t, z' | z) = \frac{1}{\sqrt{2\pi\sigma_{Gro}(a,t,z)}} e^{-\frac{(z' - \mu_{Gro}(a,t,z))^2}{2\sigma_{Gro}^2(a,t,z)}}$$

$$D(a, t, z' | z) = \frac{1}{\sqrt{2\pi\sigma_{Inh}(a,t,z)}} e^{-\frac{(z' - \mu_{Inh}(a,t,z))^2}{2\sigma_{Inh}^2(a,t,z)}}$$

The growth function was estimated using 488 measures of body mass for 233 females (Fig. 1a). As we expected that relationship between two successive body masses should change with age class (i.e. a yearling grows faster than any prime-aged individual), we performed two models including or not an interaction between age and body mass. We found no evidence of such an interaction between body mass and age (likelihood ratio test: $\chi^2 = 2.140$, $df = 2$, $P = 0.343$). As a consequence, the mean of the growth function, $\mu_G(a, t, z)$, was estimated from the linear mixed model between body mass z' at time $t+1$ and body mass z , age a at time t , and year and individual identity (when included) as random effects. The variance $\sigma_G^2(a, t, z)$ was estimated with a linear mixed regression using the squared residuals of the previous relationships (see Coulson 2012; Rees, Childs & Ellner 2014 for further details). As the model for the variance of the growth function was never investigated in roe deer, we selected the best model that described the data using the Akaike information criterion. We fitted four models: a model including an effect of age and body mass, a model including an effect of age, a model including an effect of body mass and an intercept-only model. The variance of the growth function was best fitted by a model with an effect of age (all $\Delta AIC > 3$).

$$\mu_G(a, t, z) = \alpha_{\mu_G}(a, t) + \beta_{\mu_G} * z(t) + \epsilon_{Y,\mu_G} + \epsilon_{I,\mu_G},$$

with $\epsilon_{Y,\mu_G} \sim N(0, s_{Y,\mu_G}^2)$, $\epsilon_{I,\mu_G} \sim N(0, s_{I,\mu_G}^2)$.

$$\sigma_G^2(a, t) = \alpha_{\sigma_G^2}(a, t) + \epsilon_{Y,\sigma_G^2} + \epsilon_{I,\sigma_G^2},$$

with $\epsilon_{Y,\sigma_G^2} \sim N(0, s_{Y,\sigma_G^2}^2)$, $\epsilon_{I,\sigma_G^2} \sim N(0, s_{I,\sigma_G^2}^2)$.

The inheritance function was defined similarly to the growth function. The regression between mother and offspring body mass was performed on 109 offspring from 64 mothers, and an additive effect of sex was included in the model to keep only the intercept linking mothers to female fawns (Fig. 1b, Table S1). By visual inspection, we could suspect that offspring body mass deviates from a Gaussian distribution. However, a Kolmogorov–Smirnov test did not lead us to reject the hypothesis that the distribution was Gaussian (inheritance: $D = 0.087$, $P = 0.379$). The variance of the inheritance function was best fitted using a model with an intercept only (all $\Delta AIC > 1$).

We recorded the parameters (intercepts, slope and variances of the random effects) of each function to parameterize IPMs. We created 200 body mass classes between 1 and 44 kg, the

heaviest female roe deer recorded being 32 kg. The matrices contained 12 ages (with similar survival, growth, recruitment and inheritance within a given age class). The last age class pooled together all females older than 11 years (senescent females). Consequently, our matrix \mathbf{A} had 2400 (12×200) columns and rows (see Appendix S1). The outputs of the IPM describe the population dynamics: the population growth rate, the net reproductive rate and the generation time. These parameters were estimates that were averaged over years as we used year as a random effect to parameterize the functions and build an IPM that does not vary over years. All statistical analyses were performed with the software R using code (see Appendix S2) based on Easterling, Ellner & Dixon (2000) and Coulson, Tuljapurkar & Childs (2010).

IPM MODEL: MODELLING UNMEASURED INDIVIDUAL DIFFERENCES

The first analysis that can be done to investigate the influence of unmeasured individual differences on population growth involves constructing IPMs using statistical functions identified from generalized linear mixed models with, and then without, individual identity included as a random intercept. For example, the recruitment function could take two forms:

without unmeasured individual differences:

$$M_0(a, t, z) = f(\alpha_0(a, t) + \beta_0 * z(t) + \epsilon_Y) \text{ with } \epsilon_Y \sim N(0, s_Y^2),$$

where $\alpha(a, t)$ is the intercept, β is the slope linking recruitment to body mass, and s_Y^2 is the variance of the random effect of year of the recruitment function. f represents a link function.

including unmeasured individual differences:

$$M_I(a, t, z) = f(\alpha_I(a, t) + \beta_I * z(t) + \epsilon_Y + \epsilon_I) \text{ with } \epsilon_I \sim N(0, s_I^2),$$

where s_I^2 is the variance of the random effect of individual identity on the intercept of the recruitment function.

The second analysis that can be performed is a perturbation analysis by adding P_I to the intercept of one of the four functions, corresponding to a change in the average of the unmeasured trait(s) among individuals within the population. For instance, the recruitment function becomes:

$$M_I(a, t, z) = f(\alpha_I(a, t) + \beta_I * z(t) + \epsilon_Y + P_I + \epsilon_I)$$

The influence of unmeasured individual differences on population dynamics can be assessed by comparing situations in which P_I represents a hypothetical population consisting of high ($P_I > 0$) or low ($P_I < 0$) average quality of individuals within the population (Coulson 2012).

When applied to recruitment, these perturbations will impact the first rows of the matrix \mathbf{A} (see Appendix S1) where each entry can be defined by a line corresponding to the age a' and mass z' and a column corresponding to the age a and mass z :

$$A(a' = 1, z', a, z) = D_I(a, t, z' | z, P_I = 0) M_I(a, t, z, P_I \neq 0).$$

Similarly, when the inheritance function is perturbed, each entry becomes:

$$A(a' = 1, z', a, z) = D_I(a, t, z' | z, P_I \neq 0) M_I(a, t, z, P_I = 0).$$

When the growth or the survival functions are perturbed, all entries of the matrix for which $d' > 1$ will be perturbed. We can perturb each function independently, or we can perturb all functions simultaneously. These perturbations assume populations consisting of individuals with an average value of performance P_I .

ANALYSIS

First, we investigated the effects of mass and age structures on population dynamics without modelling unmeasured individual differences. We built four different matrix models containing different age structures and excluding any relationship between the different functions and body mass (see Table 1). The most complex model included four age classes as described in this population (Gaillard *et al.* 1998a): yearlings (i.e. 1-year-old females that do not breed in roe deer, Gaillard *et al.* 1992), prime-aged adults (2–7 years), old (8–11 years) and senescent females (>11 years with reduced survival and reproductive performance). Then, we simplified this model to investigate the influence of age structure on population dynamics. The third model contained three age classes: yearlings, prime-aged adults (2–7 years) and senescent females (>7 years). The second model contained only two age classes: yearlings and adult females (>1 year). The simplest model had no age structure. We examined the effects of age-structure by comparing survival and recruitment, population growth rate, net reproductive rate and generation time with the most complex model.

For the following analyses, we selected the most parsimonious age-structured model: the model with the minimum number of age classes that gave the same parameters describing the population dynamics as our most complex model describing reliably (based on previous detailed analyses of age-dependent demography in the focal population, e.g. Festa-Bianchet, Gaillard & Côté 2003; Gaillard *et al.* 2013) the demographic rates of our population. Then, we investigated the influence of the mass structure by comparing a matrix model (including the most parsimonious age structure) and an IPM including the influence of body mass in addition to the influence of age. From this IPM, we estimated the asymptotic population growth rate (λ), the reproductive values and the stable age-size distribution, the net reproductive rate (R_0) and the cohort generation time (T_c) and compared it to the result of the matrix model. We also estimated mean body mass and mean survival and recruitment rates across all ages and body masses from this IPM (Coulson, Tuljapurkar & Childs 2010; Coulson 2012).

We next performed an elasticity analysis using the mass- and age-structured IPM without modelling unmeasured individual differences to identify the body mass class that most influences the population growth rate. Elasticity measures the proportional

change in the population growth rate generated by a proportional perturbation of the matrix entries. We calculated elasticities at the level of the matrix entries (Caswell 2001). Then, we summed elasticities over body mass classes to obtain elasticities for each age class.

Second, we used IPMs to model unmeasured individual differences (model 6, Table 1, R code is provided in Appendix S2). As described in the section on modelling unmeasured individual differences, we first compared the parameters describing the population dynamics estimated from an IPM including only age and mass structures to the ones estimated from an IPM that also included unmeasured individual differences. Second, to look at the relative influence of unmeasured individual differences in each function, we performed a perturbation analysis and compared the dynamics of populations characterized by a median average individual quality ($P_I = 0$ in all functions), a high average individual quality for this given function ($P_I = 0$ in all functions except that with $P_I = Q_I$) or a low average individual quality for this given function ($P_I = 0$ in all functions except that with $P_I = -Q_I$). For instance, the influence of unmeasured individual differences in the realized fertility function was investigated by setting $P_I = 0$ in the growth, twinning rate, survival and inheritance functions and successively $P_I = Q_{I,F}$ and $P_I = -Q_{I,F}$ in the realized fertility function. We estimated $Q_{I,F}$ by simulating the individual intercept representing the average individual quality value in realized fertility of populations of 250 individuals using a normal distribution with mean 0 and standard deviation $s_{I,F}$ (standard deviation of the component for unmeasured individual difference estimated from the generalized linear model of realized fertility). $Q_{I,F}$ was the third quartile (and so $-Q_{I,F}$ was the first quartile) of the distribution of the average individual quality values of 500 000 simulated populations. It is not realistic to consider that a population with a high average individual quality will be constituted only by high-quality individuals because in any population, there is always a distribution of individual quality. The question is thus how much the average quality of individuals within a population varies across environmental conditions. This is especially important to compare reliably the influence of individual heterogeneity with that of environmental heterogeneity in population dynamics. As a consequence, we needed to take into account how often a 'good population' occurs. We repeated this analysis for each function separately. Then, we investigated how two populations either of high (with $P_I = Q_I$) or of low (with $P_I = -Q_I$) average individual quality (i.e. high or low performance for all demographic rates) for all functions differed in terms of population growth rate, net recruitment rate and generation time.

Finally, we compared the perturbations generated by unmeasured individual differences to those generated by yearly variation

Table 1. Influence of the age and body mass structures and unmeasured individual differences on parameters describing the dynamics of a roe deer population, France

Model	$\log(\lambda)$	R_0	T_c	Sur	Rec	LE
1 Yr + no age	0.121	2.289	2.974	0.751	0.570	1.012
2 Yr + 2 age classes	0.056	1.738	4.270	0.758	0.380	3.813
3 Yr + 3 age classes	0.075	2.023	4.071	0.800	0.389	4.231
4 Yr + 4 age classes	0.076	2.042	4.104	0.801	0.389	4.275
5 Yr + 3 age classes + body mass	0.053	1.749	4.540	0.766	0.365	4.152
6 Yr + 3 age classes + body mass +ID	0.054	1.763	4.540	0.767	0.365	4.165

ID, unmeasured individual differences; Sur, survival; Rec, recruitment; LE, life expectancy at 8 months of age.

in environmental conditions, by adding an average value of year quality P_Y to the intercept of each function. P_Y was successively set to $P_Y = Q_Y$ (favourable year) and $P_Y = -Q_Y$ (unfavourable year) with $P_I = 0$ in both cases. We simulated a distribution of 500 000 years using a normal distribution of mean 0 and standard deviation s_Y (standard deviation of the component for year, different for each function). Q_Y was the third quartile of this distribution. As for unmeasured individual differences, we altered the intercept (and not the slope) in each function successively and then in all functions at the same time.

Results

EFFECTS OF AGE AND MASS STRUCTURES

The parameters describing the population dynamics were similar for models incorporating either three or four age classes in models of survival, growth, recruitment and inheritance ($\log(\lambda_4) = 0.076$ vs. $\log(\lambda_3) = 0.075$, $R_{04} = 2.042$ vs. $R_{03} = 2.023$ and $T_{c4} = 4.104$ vs. $T_{c3} = 4.071$ for four and three age classes, respectively, Table 1, models 4 and 3). While models with one or two classes of older females provided similar results, the model without any senescence (model 2, Table 1), and even more the model lacking a yearling class (i.e. model with no age, 1), led to markedly different results compared to the model with three age classes. When using two age classes (yearling vs. adult females, model 2), $\log(\lambda)$ and R_0 decreased by 25 and 14%, respectively, whereas T_c increased by 5% (Table 1) compared with a model including three age classes, likely because of a shorter life expectancy (by 5 months) in a model with only two age classes (Table 1). In a model without any effect of age (model 1), all individuals can potentially reproduce, so the mean recruitment increased by 46% compared to a model with three age classes, leading R_0 and $\log(\lambda)$ to increase (13 and 61%, respectively, Table 1). We therefore selected the model with three age classes for the following analyses.

To investigate the influence of the mass structure on population dynamics, we compared the model with three age classes (model 3, Table 1) to an IPM including body mass in addition to age (model 5). The third model excluding the effect of body mass overestimated both the population growth rate (Table 1, $\log(\lambda_3) = 0.075$ vs. $\log(\lambda_5) = 0.053$ for model 5) and the net reproductive rate ($R_{03} = 2.023$ vs. $R_{05} = 1.749$) and underestimated the generation time ($T_{c3} = 4.071$ vs. $T_{c5} = 4.540$) compared to the IPM including the influence of individual body mass (model 5). This high population growth rate was a consequence of an overestimation of recruitment (0.389 vs. 0.365) due to the nonlinear relationship between body mass and the realized fertility (Fig. 1d).

The elasticity analysis performed on model 5 (including body mass and age) revealed that survival among prime-aged females had the highest potential impact on the population growth rate ($e_{Spa} = 0.51$, Fig. S1a.). Relative perturbations in survival among yearlings and recruitment

among prime-aged females also had substantial potential impact on λ_5 ($e_{Sy} = 0.24$ and $e_{Rpa} = 0.23$, respectively). However, survival and recruitment among senescent females only weakly influenced λ_5 (e_{Ssen} and $e_{Rsen} < 0.02$). Among prime-aged females, the elasticities were highest for survival and recruitment of 23kg (Fig. S1b) and 23.5kg females, respectively.

INFLUENCE OF UNMEASURED INDIVIDUAL DIFFERENCES

We built IPMs including unmeasured individual differences in addition to body mass and age. The variance of the random intercept of individual identity was estimated to be zero in the mean of the growth function, with age explaining most of the observed differences among individual growth rates (the effect of individual identity explained 62, 33, and 0% of the variation of individual growth in a model including no age and no body mass, a model including mass but no age and a model including body mass and three age classes, respectively). No heterogeneity was detected in the survival function. Using a frailty model, we found no detectable individual heterogeneity in the survival function ($\chi^2 = 1.57$, $df = 1$, $P = 0.210$). Using a generalized linear mixed model and the MCMCglmm package, we found estimates of the fixed effects similar to the ones found using a frailty model or a generalized linear mixed model fitted with the lme4 package. However, the variance of the individual random effect was highly variable among the different runs, a two-fold variation from 0.07 to 0.15 with very large confidence intervals at 95%: [0.0002 0.5], compared to those obtained for fixed parameters. We thus parameterized our IPM using the results of the generalized linear mixed model returned by lme4, excluding the random individual effect. We analysed the influence of unmeasured individual differences on population dynamics only in realized fertility, twinning rate and inheritance functions.

Changes in slope of body mass were high when comparing models including or not unmeasured individual differences (6–23% of difference) for realized fertility, twinning rate and inheritance functions. However, variations in population growth rate, net reproductive rate and generation time were small when unmeasured individual differences were corrected for in the statistical analyses used to identify the functions for the IPMs (Table 1, models 5 and 6). The reproductive value as a function of body mass remained similar in models with and without unmeasured individual differences (Fig. 2b), whereas the stable age-size distribution differed between these two models (Fig. 2a). The distribution of yearling body mass (first ‘hump’) can be clearly distinguished from the distribution of adult body mass when including unmeasured individual differences (model 6 and 5, Fig. 2a).

Because unmeasured individual differences affected parameter estimation, we explored its potential impact on population dynamics by using the variance components

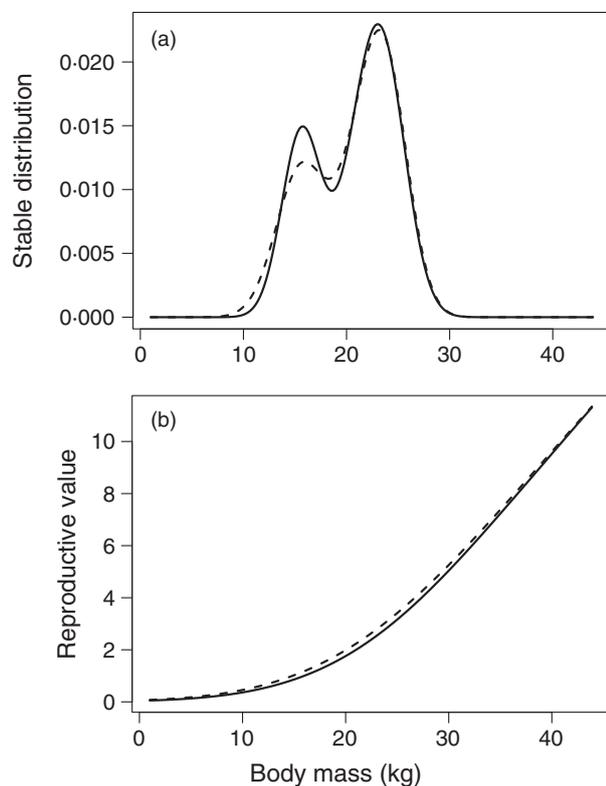


Fig. 2. Stable body mass distributions (a) and reproductive values (b) modelled using three age classes and including (model 6, Table 1, solid lines) or not (model 5, Table 1, dashed line) unmeasured individual differences.

estimated from the generalized linear mixed effect models to construct populations characterized by low, mean and high average quality of individuals (model 6 with $P_I = -Q_I$, $P_I = 0$ or $P = Q_I$) in each function separately, and then in all functions at the same time (except the survival and mean of the growth functions in both cases). In all cases, populations consisting of high vs. low average individual quality exhibited small changes in parameters describing population dynamics (Fig. 3). The population growth rate (on a logarithmic scale) and the net reproductive rate decreased by 6.3% and 3.2%, respectively, and the generation time increased by 0.6% from a high ($P_I = Q_I$) to a low ($P_I = -Q_I$) performance population, on average (model 6 with $P_I \neq 0$ in all functions). Such differences were mostly (60%) driven by changes in mean recruitment. The realized fertility function contributed slightly more to changes in parameters describing population dynamics than the twinning rate function (34 and 26%, respectively). The presence of positive co-variation among individual intercepts across functions had almost no effect on model parameters describing population dynamics (Fig. 3).

The perturbation of population growth rate produced by variation in year quality was higher than that produced by variation in unmeasured individual differences. The population growth rate (on a logarithmic scale) and the net reproductive rate decreased by 74 and 46%, respectively,

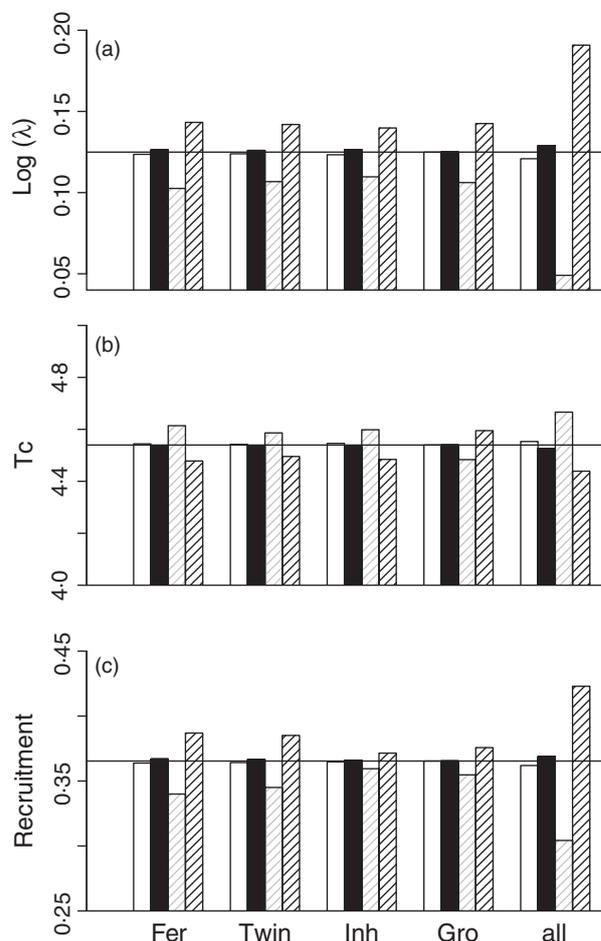


Fig. 3. Influence of unmeasured individual differences compared to the influence of variation in environmental conditions on three parameters describing population dynamics: the population growth rate ($\log(\lambda)$, a), the cohort generation time (T_c , b) and the mean recruitment rate (c). Two populations of different (high (black) and low (white)) average performance were compared to two populations facing favourable (black hatched) and unfavourable (grey hatched) years using the model 6 (Table 1). Median parameters are represented by a black solid line. Each function was successively perturbed (realized fertility, twinning rate, inheritance and growth) before being all perturbed at same time (all).

and the generation time increased by 5% between favourable and unfavourable years when environmental conditions affected all functions (Fig. 3). As for unmeasured individual differences, the recruitment function was the target of changes in environmental conditions. When only realized fertility or twinning rate was affected, the population growth rate (on a logarithmic scale) decreased by 28 and 25%, respectively, between favourable and unfavourable years (when survival, inheritance or growth were affected, $\log(\lambda)$ decreased by 0, 21 and 25%, respectively).

Discussion

Although the recruitment and inheritance functions were clearly influenced by unmeasured individual differences

(modelled as random effects on the intercept of these functions), the parameters describing the population dynamics from our models were not. The age structure, mass structure and yearly variation all affected the population dynamics to a much larger extent than unmeasured individual differences.

Let us replace individual random effects with an important but most often unmeasured life-history trait, birth date. Birth date is a typical trait that is strongly linked to individual quality because individual fitness is higher for early-born than for late-born individuals (Plard *et al.* 2015). However, the influence of birth date on population dynamics is much lower than the influence of environmental variations in roe deer because the distribution of individual birth dates does not change over years (Plard *et al.* 2014a), whereas climate change has strong negative influence on the population growth rate (Gaillard *et al.* 2013). By including birth date in addition to body mass and age in the different functions of the IPMs (Table S2 for the estimates of the different models of demographic rates including birth date or not on a smaller data set including only individuals with known birth date), the estimated intercepts and slope of these functions do not change much compared to results obtained when using individual random effects. There are two reasons for this: first, birth date is a normally distributed trait in roe deer (Plard *et al.* 2013) and should be correctly modelled using random individual effects. Second and more importantly, most of the influence of birth date on future reproductive abilities and on fitness is mediated through body mass (Plard *et al.* 2015). Indeed, early-born females have a higher fitness than late-born females because they reach a higher body mass as adults. Heterogeneity in body mass should approximately reflect heterogeneity in individual birth date, and adding birth date in a model of population dynamics using body mass does not substantially change the parameters describing the population dynamics.

In other words, the influence of heterogeneity created by some unmeasured variables (that can be important for each specific demographic rate) on population dynamics can be negligible if the individual differences in some measured variables (body mass and age) already capture a large part of the individual heterogeneity existing in the population or if the individual distribution of this unmeasured trait does not change much with time. Our results support two previous studies that included unmeasured individual differences in IPMs. In the Soay sheep, *Ovis aries*, when accounting for body mass, correcting for random effects of individual identity had less influence on the population dynamics than correcting for population density (Coulson 2012). Likewise, Rees *et al.* (1999) found that unmeasured individual variation (modelled as an individual random effect on the intercept) in growth and mortality rates had only small impacts on the population dynamics of a plant species, *Onopordum illyricum*.

Unmeasured individual differences have been reported to be a major source of variation to consider when estimating survival and reproductive parameters. Moreover, the failure to account for unmeasured individual differences can lead to biased estimates of demographic variability and the parameters describing population dynamics (Clark 2003; Kendall *et al.* 2011). Recently, Vindenes & Langangen (2015) developed an IPM including fixed individual differences, suggesting that individual heterogeneity has the potential to influence population dynamics. They, however, had no data to estimate empirically the parameter (α) through which individual differences influenced the survival function (they chose a random range for α) and so did not provide empirical evidence. Our findings indicate that in the case of roe deer, individual heterogeneity plays only a minor role in population dynamics once individual differences associated with age and body mass are accounted for, but also support Vindenes and Langangen's view that individual differences can be important to the evolution of populations in variable environments and to eco-evolutionary dynamics.

In our analysis, unmeasured individual differences influenced both the recruitment and the inheritance functions but not the mean of the growth and the survival functions. Despite the fact that heterogeneity in survival can be an important cause of variation in population dynamics (Kendall *et al.* 2011), previous studies have reported little variation in population growth rate even after correcting for individual heterogeneity in survival and growth (Rees *et al.* 1999; Coulson 2012). Nevertheless, the weak influence of unmeasured individual differences in survival could be due to an underestimation of the variance component of our model caused by our relatively low sample size ($n = 99$). Thus, we considered a hypothetical case where unmeasured individual differences influence survival to a greater extent to assess the potential impact of individual heterogeneity in survival on population dynamics (see Fig. S2). In this case, unmeasured individual differences in survival did influence the population dynamics. However, variation in environmental conditions had still a larger influence on population dynamics than unmeasured individual differences in both reproduction and survival (Fig. S2). As a consequence, species showing large individual differences in survival are expected to be more influenced by individual heterogeneity than our study species. In long-lived species, such as roe deer, adult survival varies little and is a typical case of environmental canalization (Gaillard & Yoccoz 2003). Consequently, in species showing this kind of demographic tactic, individual differences independent of age and mass are expected to have little impact on population dynamics.

The recruitment of individuals with a median mass remained similar in models that either corrected (or not) for unmeasured individual differences. As expected, light (heavy) individuals recruited fewer (more) offspring in models including unmeasured individual differences than

in models excluding them. Including unmeasured individual variation mainly impacted very light and very heavy individuals (it was the same in Coulson (2012) for Soay sheep). Population growth rate was weakly sensitive to extreme individuals as revealed by the elasticity analysis. Females weighing around 22–24 kg had the largest impact on population growth. Including unmeasured individual differences in recruitment only had a small influence on individuals with median mass, and consequently, only little influenced population growth rate.

Nevertheless, our study made two assumptions that, if not fulfilled, could have contributed to decrease the influence of unmeasured individual differences on population dynamics. First, we assumed that individual random effects reliably capture individual heterogeneity caused by unmeasured traits. This is not necessarily the case. For instance, when individual differences in the unmeasured trait follows a multinomial distribution (e.g. by displaying different groups of individuals according to their fixed quality), then individual random effects (which assume a normal distribution of individual differences) could not reliably capture such individual heterogeneity and would fail to model correctly the influence of unmeasured individual differences. However, this is not expected to occur in roe deer for which other characters known to influence individual quality follow a Gaussian distribution (like birth date in roe deer, see above). Second, we only included random effects of individual differences on the intercept of the function, but not on their slope. Krishnakumar *et al.* (unpublished results) have shown that random effects associated with slopes have a much larger and more nonlinear influence on the parameters that describe population dynamics (the generation time, the net reproductive rate and the asymptotic population growth rate) than random effects associated with intercepts. Thus, unlike random effects associated with intercepts, random effects associated with slopes do not produce the same proportional change for lighter and heavier individuals. As a result, we can expect that unmeasured individual differences are not likely to produce a major impact on model output except if these unmeasured differences interact with the measured trait when influencing the different demographic rates. Moreover, the impact of unmeasured individual differences should be more important in small populations or in populations during the process of colonization (Vindenes, Engen & Sæther, 2008) as the probability to have a population consisting mostly of low- or high- quality individuals increases in small populations.

Individual differences in demographic rates of large herbivores mostly result from differences in body mass, with heavier individuals living longer and having higher annual reproductive success than light individuals (Gaillard *et al.* 2000b). Therefore, measured individual differences in body mass and age shape most observed variation in individual fitness (Plard *et al.* 2014b). A model including heterogeneity in body mass and age

should thus capture a large proportion of individual heterogeneity within a population of large herbivore such as roe deer. Unmeasured individual differences in other traits are likely to be correlated to differences in body mass at a given age (leading to the concept of individual quality, Wilson & Nussey 2010) or to be relatively small and have only a weak effect on population dynamics. While for some species, age-dependent models can be advantageously replaced with mass-dependent models because reproduction and survival are mostly related to body mass (Sauer & Slade 1987; Gamelon *et al.* 2012), the distribution of body mass alone does not allow to estimate a reliable individual age of first reproduction in roe deer. Age variation therefore matters because yearlings are allowed to give birth before the observed age of first reproduction in roe deer (2 years) as recruitment continuously increases with body mass. Not accounting for this constraint leads to erroneous metrics of population dynamics when age structure is not explicitly included in models.

In conclusion, our study demonstrates that individual heterogeneity in age and mass generates crucial sources of individual variation that influence the dynamics of a population. On the other hand, unmeasured individual differences are important for many things, but not necessarily for all things, in this population. In a long-lived species like roe deer, the individuals constituting the population remain similar from 1 year to the next (with a generation time of about 4 years, about 25% of individuals are replaced each year). As individual quality is highly repeatable (e.g. Plard *et al.* 2013), temporal variation in average individual quality in a population of a long-lived species like roe deer should be dampened, explaining why we report only a minor influence of individual heterogeneity on population dynamics compared to the impact of age structure and yearly variation.

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Data accessibility

The data are included in the Tables S4–S8.

References

- Albon, S.D., Coulson, T.N., Brown, D., Guinness, F.E., Pemberton, J.M. & Clutton-Brock, T.H. (2000) Temporal changes in key factors and key age groups influencing the population dynamics of female red deer. *Journal of Animal Ecology*, **69**, 1099–1110.

- Aubry, L.M., Koons, D.N., Monnat, J.Y. & Cam, E. (2009) Consequences of recruitment decisions and heterogeneity on age-specific breeding success in a long lived seabird. *Ecology*, **90**, 2491–2502.
- Benton, T.G., Plaistow, S.J. & Coulson, T.N. (2006) Complex population dynamics and complex causation: devils, details and demography. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 1173–1181.
- Cam, E., Link, W.A., Cooch, E.G., Monnat, J.Y. & Danchin, E. (2002) Individual covariation in life-history traits: seeing the trees despite the forest. *The American Naturalist*, **159**, 96–105.
- Caswell, H. (1978) A general formula for sensitivity of population growth rate to changes in life history parameters. *Theoretical Population Biology*, **14**, 215–230.
- Caswell, H. (2001) *Matrix Population Models: Construction, Analysis, and Interpretation*, 2nd edn. Sinauer Associates, Sunderland, Massachusetts.
- Caswell, H. (2011) Beyond R-0: demographic models for variability of lifetime reproductive output. *PLoS ONE*, **6**, e20809.
- Clark, J. (2003) Uncertainty and variability in demography and population growth: A hierarchical approach. *Ecology*, **84**, 1370–1381.
- Coulson, T. (2012) Integral projections models, their construction and use in posing hypotheses in ecology. *Oikos*, **121**, 1337–1350.
- Coulson, T., Catchpole, E.A., Albon, S.D., Morgan, B.J.T., Pemberton, J.M., Clutton-Brock, T.H., Crawley, M.J. & Grenfell, B.T. (2001) Age, sex, density, winter weather, and population crashes in Soay sheep. *Science*, **292**, 1528–1531.
- Coulson, T.N., Tuljapurkar, S. & Childs, D.Z. (2010) Using evolutionary demography to link life history theory, quantitative genetics and population ecology. *Journal of Animal Ecology*, **79**, 1226–1240.
- Coulson, T., Macnulty, D.R., Stahler, D.R., VonHoldt, B., Wayne, R.K. & Smith, D.W. (2011) Modeling effects of environmental change on wolf population dynamics, trait evolution, and life history. *Science*, **334**, 1275–1278.
- Delorme, D., Gaillard, J.M. & Jullien, J.M. (1988) Intérêt de l'étude de la période juvénile pour le suivi de l'évolution d'une population de chevreuils (*Capreolus capreolus*). *Gibier Faune Sauvage*, **5**, 15–26.
- Easterling, M.R., Ellner, S.P. & Dixon, P.M. (2000) Size-specific sensitivity: applying a new structured population model. *Ecology*, **81**, 694–708.
- Eberhardt, L.L. (1985) Assessing the dynamics of wild populations. *Journal of Wildlife Management*, **49**, 997–1012.
- Ellner, S.P. & Rees, M. (2006) Integral projection models for species with complex demography. *The American Naturalist*, **167**, 410–428.
- Festa-Bianchet, M., Gaillard, J.M. & Côté, S.D. (2003) Variable age structure and apparent density dependence in survival of adult ungulates. *Journal of Animal Ecology*, **72**, 640–649.
- Flerov, K.K. (1952) *Fauna of USSR: Mammals Vol. 1 No. 2. Musk Deer and Deer*. Academy of Sciences of the USSR, Leningrad.
- Gaillard, J.M. & Yoccoz, N.G. (2003) Temporal variation in survival of mammals: a case of environmental canalization? *Ecology*, **84**, 3294–3306.
- Gaillard, J.M., Sempéré, A.J., Boutin, J.M., Van Laere, G. & Boisauvert, B. (1992) Effects of age and body weight on the proportion of females breeding in a population of roe deer (*Capreolus capreolus*). *Canadian Journal of Zoology*, **70**, 1541–1545.
- Gaillard, J.M., Delorme, D., Boutin, J.M., Van Laere, G., Boisauvert, B. & Pradel, R. (1993) Roe deer survival patterns: a comparative analysis of contrasting population. *Journal of Animal Ecology*, **62**, 778–791.
- Gaillard, J.M., Boutin, J.M., Delorme, D., Van Laere, G., Duncan, P. & Lebreton, J.D. (1997) Early survival in roe deer: causes and consequences of cohort variation in two contrasted populations. *Oecologia*, **112**, 502–513.
- Gaillard, J.M., Liberg, O., Andersen, R., Hewison, A.J.M. & Cederlund, G. (1998a) Population dynamics of roe deer. *The European Roe Deer: The Biology of Success* (eds R. Andersen, P. Duncan & J.D.C. Linnell), pp. 309–336. Scandinavian University Press, Oslo, Norway.
- Gaillard, J.M., Andersen, R., Delorme, D. & Linnell, J.D.C. (1998b) Family effects on growth and survival of juvenile roe deer. *Ecology*, **78**, 2878–2889.
- Gaillard, J.M., Festa-Bianchet, M., Delorme, D. & Jorgenson, J. (2000a) Body mass and individual fitness in female ungulates: bigger is not always better. *Proceedings of the Royal Society B: Biological Sciences*, **267**, 471–477.
- Gaillard, J.M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A. & Toigo, C. (2000b) Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics*, **31**, 367–393.
- Gaillard, J.M., Hewison, M.A.J., Klein, F., Plard, F., Douhard, M., Davison, R. & Bonenfant, C. (2013) How does climate change influence demographic processes of widespread species? Lessons from the comparative analysis of contrasted populations of roe deer. *Ecology Letters*, **16**, 48–57.
- Gamelon, M., Gaillard, J.M., Servanty, S., Gimenez, O., Toigo, C., Baubet, E., Klein, F. & Lebreton, J.D. (2012) Making use of harvest information to examine alternative management scenarios: a body weight-structured model for wild boar. *Journal of Applied Ecology*, **49**, 833–841.
- Gimenez, O., Viallefont, A., Charmantier, A., Pradel, R., Cam, E., Brown, C.R., Anderson, M.D., Brown, M.B., Covas, R. & Gaillard, J.M. (2008) The risk of flawed inference in evolutionary studies when detectability is less than one. *The American Naturalist*, **172**, 441–448.
- Hamel, S., Côté, S.D., Gaillard, J.M. & Festa-Bianchet, M. (2009a) Individual variation in reproductive costs of reproduction: high-quality females always do better. *Journal of Animal Ecology*, **78**, 143–151.
- Hamel, S., Gaillard, J.M., Festa-Bianchet, M. & Côté, S.D. (2009b) Individual quality, early-life conditions, and reproductive success in contrasted populations of large herbivores. *Ecology*, **90**, 1981–1995.
- Jacquemyn, H., Brys, R. & Jongejans, E. (2010) Size-dependent flowering and costs of reproduction affect population dynamics in a tuberous perennial woodland orchid. *Journal of Ecology*, **98**, 1204–1215.
- Jolles, A.E., Cooper, D.V. & Levin, S.A. (2005) Hidden effects of chronic tuberculosis in African buffalo. *Ecology*, **86**, 2358–2364.
- Kendall, B.E. & Fox, G.A. (2003) Unstructured individual variation and demographic stochasticity. *Conservation Biology*, **17**, 1170–1172.
- Kendall, B.E., Fox, G.A., Fujiwara, M. & Nogueira, T.M. (2011) Demographic heterogeneity, cohort selection, and population growth. *Ecology*, **92**, 1985–1993.
- Knape, J., Jonzén, N., Sköld, M., Kikkawa, J. & McCallum, H. (2011) Individual heterogeneity and senescence in Silvereyes on Heron Island. *Ecology*, **92**, 813–820.
- Lewis, S., Wanless, S., Elston, D.A., Schultz, M.D., Mackley, E., Du Toit, M., Underhill, J.G. & Harris, M.P. (2006) Determinants of quality in a long-lived colonial species. *Journal of Animal Ecology*, **75**, 1304–1312.
- Lindberg, M.S., Sedinger, J.S. & Lebreton, J.D. (2013) Individual heterogeneity in black brant survival and recruitment with implications for harvest dynamics. *Ecology and Evolution*, **3**, 4045–4056.
- Link, W.A., Cooch, E.G. & Cam, E. (2002) Model-based estimation of individual fitness. *Journal of Applied Statistics*, **29**, 207–224.
- van Noordwijk, A.J. & de Jong, G. (1986) Acquisition and allocation of resources: their influence on variation in life history tactics. *The American Naturalist*, **128**, 137–142.
- Nussey, D.H., Coulson, T.N., Festa-Bianchet, M. & Gaillard, J.M. (2008) Measuring senescence in wild animal populations: towards a longitudinal approach. *Functional Ecology*, **22**, 393–406.
- Nussey, D.H., Coulson, T., Delorme, D., Clutton-Brock, T.H., Pemberton, J.M., Festa-Bianchet, M. & Gaillard, J.M. (2011) Patterns of body mass senescence and selective disappearance differ among three species of free-living ungulates. *Ecology*, **92**, 1936–1947.
- Peripato, A.C., de Brito, R.A., Vaughn, T.T., Pletscher, L.S., Matioli, S.R. & Cheverud, J.M. (2002) Quantitative trait loci for maternal performance for off-spring survival in mice. *Genetics*, **162**, 1341–1353.
- Plard, F., Gaillard, J.M., Bonenfant, C., Hewison, A.J.M., Delorme, D., Cargnelutti, B., Kjellander, P., Nilsen, E.B. & Coulson, T. (2013) Parturition date for a given female is highly repeatable within five roe deer populations. *Biology Letters*, **9**, 20120841.
- Plard, F., Gaillard, J.M., Coulson, T., Hewison, A.J.M., Delorme, D. & Bonenfant, C. (2014a) Mismatch between birth date and vegetation phenology slows the demography of roe deer. *PLoS Biology*, **12**, e1001828.
- Plard, F., Gaillard, J.M., Coulson, T., Hewison, A.J.M., Delorme, D., Nilsen, E.B. & Bonenfant, C. (2014b) Long-lived and heavier females give birth earlier in roe deer. *Ecography*, **37**, 241–249.
- Plard, F., Gaillard, J.M., Coulson, T., Hewison, A.J.M., Douhard, M., Klein, F., Delorme, D., Warnant, C., Bonenfant, C. (2015) The influence of birth date via body mass on individual fitness in a long-lived mammal. *Ecology*, in press
- van de Pol, M. & Verhulst, S. (2006) Age-dependent traits: A new statistical model to separate within- and between-individual effects. *The American Naturalist*, **167**, 766–773.
- Rees, M., Sheppard, A., Briese, D. & Mangel, M. (1999) Evolution of size dependent flowering in *Onopordum illyricum*: A quantitative assessment

- of the role of stochastic selection pressures. *The American Naturalist*, **154**, 628–651.
- Rees, M., Childs, D.Z. & Ellner, S.P. (2014) Building integral projection models: a user's guide. *Journal of Animal Ecology*, **83**, 528–545.
- Reid, J.M., Arcese, P., Cassidy, A.L.E.V., Hiebert, S.M., Smith, J.N.M., Stoddard, P.K., Marr, A.B. & Keller, L.F. (2004) Song repertoire size predicts initial mating success in male song sparrows, *Melospiza melodia*. *Animal Behaviour*, **68**, 1055–1063.
- Rose, K.E., Rees, M. & Grubb, P.J. (2002) Evolution in the real world: stochastic variation and the determinants of fitness in *Carlina vulgaris*. *Evolution*, **56**, 1416–1430.
- Sauer, J.R. & Slade, N.A. (1987) Size-based demography of vertebrates. *Annual Review of Ecology and Systematics*, **18**, 71–90.
- Steiner, U.K., Tuljapurkar, S. & Orzack, S.H. (2010) Dynamic heterogeneity and life history variability in the kittiwake. *Journal of Animal Ecology*, **79**, 436–444.
- Stopher, K.V., Pemberton, J.M., Clutton-Brock, T.H. & Coulson, T. (2008) Individual differences, density dependence and offspring birth traits in a population of red deer. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 2137–2145.
- Therneau, T.M. (2014) Package 'survival'.
- Tuljapurkar, S., Steiner, U.K. & Orzack, S.H. (2009) Dynamics heterogeneity in life histories. *Ecology Letters*, **12**, 93–106.
- Vaupel, J.W. & Yashin, A.I. (1985) Heterogeneity's ruses: some surprising effects of selection on population dynamics. *The American Statistician*, **39**, 176–185.
- Vaupel, J.W., Manton, K.G. & Stallard, E. (1979) The impact of heterogeneity in individual frailty on the dynamics of mortality. *Demography*, **16**, 439–454.
- Vindenes, Y. & Langangen, Ø. (2015) Individual heterogeneity in life histories and eco-evolutionary dynamics. *Ecology Letters*, **18**, 417–432.
- Vindenes, Y., Engen, S. & Sæther, B.E. (2008) Individual heterogeneity in vital parameters and demographic stochasticity. *The American Naturalist*, **171**, 455–467.
- Wilson, A.J. & Nussey, D.H. (2010) What is individual quality? An evolutionary perspective. *Trends in Ecology & Evolution*, **25**, 207–214.

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Supporting Information

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

Appendix S1. Description of matrices.

Appendix S2. R Code used to run the model 6 and simulate populations of high- and low-quality individuals on average.

Figure S1. Elasticity analysis of a population using an IPM with three age classes.

Figure S2. Influence of unmeasured individual differences compared to the influence of variation in environmental conditions on the population growth rate ($\log(\lambda)$) in IPM including unmeasured individual differences and environmental heterogeneity in survival with $\sigma_{I,S} = \sigma_{Y,S} = 0.5$ (A), $\sigma_{I,S} = \sigma_{Y,S} = 1$ (B) and $\sigma_{I,S} = \sigma_{Y,S} = 2$ (C) in addition to unmeasured individual differences estimated in the other functions for the roe deer population of Trois Fontaines.

Table S1. Parameters of the IPMs including a possible age and body mass structure, an effect of year and a possible effect of unmeasured individual differences.

Table S2. Estimates of the parameters of the vital functions including an age and body mass structure and including (b,c) or not (a) individual birth date (b) or individual random effect (c).

Table S3. Estimates of the slope linking body mass to the different functions of the IPM.

Table S4. Data used to parameterize the realized fertility function.

Table S5. Data used to parameterize the twinning rate function.

Table S6. Data used to parameterize the survival function.

Table S7. Data used to parameterize the growth function.

Table S8. Data used to parameterize the inheritance function.